The EMPIRE JOURNAL of EXPERIMENTAL AGRICULTURE

VOLUME XXVI

OXFORD
AT THE CLARENDON PRESS
1958

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Plate 6 (Fig. 5c), facing p. 321:—

for Damage more severe than in *h*
but less than in *g*.
Surface less deformed than in *g*

read Damage more severe than in *b*
but less than in *a*.
Surface less deformed than in *a*

Page 325, Table 2, line 1:—

for 5·9

read 25·9

Page 326, lines 23 and 24:—

for and recordings were made twice daily at 11 a.m. and 3 p.m. on three consecutive days,

read and three consecutive recordings were made twice daily at 11 a.m. and 3 p.m.,

Page 328, Table 4, line 6:—

for 6197

read 6187

EAST AFRICAN WORK ON BREEDING MAIZE RESISTANT TO THE TROPICAL AMERICAN RUST, *PUCCINIA POLYSORA*

H. H. STOREY AND AUDRIE K. HOWLAND (RYLAND),[1]
J. S. HEMINGWAY,[2] J. D. JAMESON AND B. J. T. BALDWIN,[3]
H. C. THORPE AND G. E. DIXON[4]

WITH PLATE I

Summary

Since 1952 *Puccinia polysora* Underw. has become widespread in maize in the tropical areas of East Africa, and severe attacks have been shown to reduce yield greatly. Two physiologic races have been recognized, 'EA.1' being today the prevalent race in the field and 'EA.2' being known as yet only in the Muguga glasshouses.

Experimental infection trials in glasshouses at Muguga, Kenya, failed to demonstrate resistance in any African maize variety; but among maizes imported from Central America and the Caribbean plants were found that showed the hypersensitive type of resistance. From these, lines were bred that were pure for either of two genes: **Rpp1** conferred high resistance to Race EA.1 but none to EA.2; while **Rpp2** conferred a lesser, but effective, resistance equally to both rust races.

Field breeding at three stations in East Africa was successful in incorporating each of these genes separately in locally adapted maize varieties; and considerable bulks of pure-breeding resistant maizes were expected to become available during 1957 and later years.

Puccinia polysora Underw. first became prominent in the literature of plant pathology when, in the years following 1949, it caused heavy losses in the maize crops of tropical West Africa [1]. This species had, however, been recognized by Cummins [2] as parasitic on maize as early as 1941, when he distinguished it from the cosmopolitan maize-rust fungus, *Puccinia sorghi* Schw. By examining herbarium specimens, Cummins showed that *P. polysora* was widely distributed and long established in tropical and subtropical America. On the other hand, all maize-rust specimens collected in Africa prior to 1949 appeared to be *P. sorghi* [1].

First reports of *P. polysora* in East Africa were in 1952 [3, 4]. Warned, however, by West African experience, an East African committee of plant research workers, under the chairmanship of Sir Joseph Hutchinson, had already planned co-operative research to combat the expected outbreak. The basis of the plan was the expectation that maizes resistant to *P. polysora* would have evolved in Central America, the home of the fungus (as Stanton and Cammack in fact found in West Africa [5]). If genes for resistance could thus be obtained, it was likely that they could be transferred to maize varieties adapted to East African conditions.

[1] East African Agriculture and Forestry Research Organization.
[2] Tanganyika Agricultural Corporation.
[3] Uganda Department of Agriculture.
[4] Kenya Department of Agriculture.

[Empire Journ. of Exper. Agric., Vol. 26, No. 101, 1958.]

In general this expectation was realized. East African maize varieties showed no resistance when tested in West Africa [6] or, after 1952, in East Africa. But in Central American and Caribbean types imported by the East African Agriculture and Forestry Research Organization genes for resistance were demonstrated by glasshouse experiments at Muguga, Kenya; and during 1953 it was possible not only to distribute to the breeders seed of the most promising importations and of first-generation selfs and crosses, but also to provide them with basic genetic information to guide their work [7]. From this start, field breeding was done at the Nachingwea station of the Tanganyika Agricultural Corporation, at two Agricultural Department stations near the Kenya coast, and at the Kawanda station of the Uganda Department of Agriculture. By 1956 it had advanced to the point where pure resistant maize lines, carrying a high proportion of local genes, were becoming available for bulking.

The Occurrence of P. polysora *in East Africa*

Puccinia polysora was first recognized at sites inland (Kilosa, Tanganyika, 1,600 ft., Wallace *in litt.*; and Taveta, Kenya, 2,500 ft., Nattrass [3]), but its main development has been in tropical areas at low altitude. It is now widely distributed throughout the coastal belt and hinterland of East Africa and in parts of Uganda. Its altitudinal limit has not been defined; but it has not yet been recorded from the important maize-growing areas in the Kenya Highlands nor even from those lying to the east and north of Lake Victoria, despite its presence at similar altitudes in Uganda on the west side of the lake.

Experience in East Africa is that the disease attains its full severity in maize at or after flowering. Such plants may be heavily affected, with uredosori (and rarely teleutosori) crowded on all leaves, plentiful on leaf- and cob-sheaths and sometimes on the stems. But since this attack is late, a total loss of crop has never been reported, and it is often not possible without detailed observation to decide what loss has been incurred. However, exact experiments at Nachingwea, in which plots of 'Katumbili' maize were protected—although not with full success—by heavy sulphur-dustings, showed the yield of unprotected plots to be only 67 per cent. of that of the protected ones [8].

Up to 1956 two physiologic races of *P. polysora* have been recognized in East Africa. Race 'EA.1' was that first found, and collections made in 1952 in Zanzibar, Tanganyika, and Uganda all appeared to be identical. In 1955, however, a second race, 'EA.2', distinguishable by its reaction on certain pure-breeding maize lines, appeared in the Muguga glasshouses [9]. The origin of Race EA.2 remains unexplained; it has not yet been certainly identified anywhere in the field.

Experimental Studies of Rust Resistance in the E.A.A.F.R.O. Glasshouses

Experimental work was initiated by E.A.A.F.R.O. at Muguga, Kenya, which lies at 6,800 ft. altitude and has a temperate climate. *Puccinia polysora* has never been encountered on field maize in this region,

although *P. sorghi* is prevalent. Nevertheless, in glasshouses receiving artificial heat when the temperature fell below 70° F., *P. polysora* developed strongly on susceptible maize seedlings inoculated with it by the technique developed.

Experimental methods are fully described in a paper now in preparation (by H. H. S. and A. K. H.). Uredospores, taken from recently developed sori on maize, were spread on the undamaged surface of two leaves of 3-leaf maize seedlings, using 0·25 per cent. gelatine solution as a wetting agent; the inoculated plants were incubated for 24–48 hours in a saturated atmosphere maintained by covering with polythene hoods, and thereafter in the open glasshouses; and recorded for rust reactions at 10, 14, and 18 days. Seedlings selected in these tests were transplanted to 4-gallon containers and grown to maturity in a large glasshouse, and selfed or crossed as required. In the glasshouses work could continue throughout the year, without dependence on season.

The Search for Resistance in African Maizes

All of the following sixty-eight maize varieties from African sources were given seedling tests against Race EA.1 and many against EA.2:

From East Africa: Kitale Flat White (3 samples); North Nyanza (3); Durum (2); Yellow Coast; Peruvian Yellow (6); K8; Muratha; Katumbili (5); miscellaneous native varieties (2).
From S. Rhodesia: inbred lines (7); double hybrids (3).
From Nyasaland: native varieties (10); hybrids of native varieties (4).
From the Union of S. Africa: standard varieties (20).

All gave the characteristic susceptible reaction (Plate 1, fig. 3), except that some inoculations failed for reasons believed to be technical and in some plants chlorosis around the sori was more marked than normal.

This failure of our tests to reveal any resistance among African varieties is in conformity with evidence of the West African Maize Rust Research Unit [6]. There are, however, suggestions that an ability to escape severe infection, or alternatively to tolerate infection, may occur in some maizes. Thus Ellis [10] reports that certain native maizes in Nyasaland, though attacked by *P. polysora*, show no significant reduction in yield. The varieties to which he refers were inoculated in our glasshouses by several different methods, but their reactions were typical of susceptibility and not detectably different from those in a Rhodesian hybrid, which in Ellis's experiments had shown a large effect from rust infection. There are indications that some American types may show similar field resistance although susceptible as seedlings.

If an inherited ability to escape rust infections or to tolerate its effect exists, it is not revealed by the methods of juvenile testing.

The Search for Resistance in American Maizes

In all, 203 maize varieties and lines were obtained from the following sources, through the co-operation of the authorities named.

6—from the Rockefeller Institute, Mexico City, through Dr. W. R. Stanton, West African Maize Rust Research Unit, Ibadan, Nigeria. AFRO Nos. 22–27.

19—from Dr. L. M. Roberts, The Rockefeller Foundation, Estacion Agricola Experimental, Medellin, Colombia. AFRO Nos. 28–46.

9—from Dr. A. J. Ullstrup, Purdue Agricultural Experiment Station, Lafayette, Indiana, U.S.A. AFRO Nos. 47–55.

118—from Dr. W. L. Brown, through the Principal, Imperial College of Tropical Agriculture, Trinidad. AFRO Nos. 56–173.

51—from Dr. Mario Gutierrez G., Inter-American Institute of Agricultural Sciences, Turrialba, Costa Rica. AFRO Nos. 225–75.

All the above, with the exception of a few believed to be duplicates of numbers received from other sources, were given seedling tests against rust Race EA.1. The majority showed only the susceptible reaction; but in a number some plants appeared to be resistant. No variety or line, as received, was homozygous for resistance.

Occasionally in these tests, as in those of African maizes, the inoculated leaves showed no reaction; but, by repeating tests and by breeding from the unaffected plants, the authors satisfied themselves that the observation was due only to accidental escape. True immunity from infection as seedlings does not appear to exist in any of the maizes the authors have tested.

The resistance encountered took the form of a hypersensitive reaction by the plant to the fungus mycelium, such as is well known with the rusts of wheat and other small cereals (e.g. Chester [11]). This hypersensitive reaction is believed to deprive the mycelium of nutrients, confining it to a limited area of dead tissue and preventing or greatly reducing spore production. The reactions of experimental seedlings were classified according to the following system, adapted from that of the wheat breeders [12].

Resistant. Class '01'—chlorotic-necrotic lesions, never producing sori (Plate 1, fig. 1).

Class '1'—starting as '01', but later producing small sori on the lesions. The size and frequency of the sori are recorded by appended signs, from '— —' to '+ +' (Plate 1, fig. 2).

Susceptible. Class '4'—no necrosis of the leaf; amount of chlorosis variable but usually slight; sori erupting from leaf tissue that appears otherwise nearly normal and rapidly enlarging (Plate 1, fig. 3).

Intermediate. Class 'X'—a reaction intermediate between '1' and '4', typically showing lesions with small sori chracteristic of '1' and, in addition, medium or large sori erupting from mainly green tissue.

It was supposed that if the reaction of the plant did not change with growth, Class '01' would represent effective immunity in the field; while Class '1', in which spore production was very much less than in Class '4', could afford a useful field resistance. The authors' first action was therefore to select the '01' plants, and the '1' plants with a preference

for those showing the least soral development, to self these selections and to cross them with local susceptible maizes.

Two of the authors (H. H. S. and A. K. H.) are publishing elsewhere the results of a genetic analysis. It has led to the conclusion that two major genes (or possibly more than two) control the hypersensitive reaction; that one, designated **Rpp1**,[1] confers ability to react '01' against rust Race EA.1 in juvenile tests but confers no resistance to Race EA.2; while gene **Rpp2** gives a range of reactions from '01' (lesions larger and generally more necrotic than those due to **Rpp1**) to '1+ +', and sometimes 'X', against both races.

While **Rpp1** is fully dominant, **Rpp2** is incompletely dominant and plants heterozygous for it tend to give more severe reactions than those homozygous. There are indications also that minor genes may influence the severity of the **Rpp2** reaction.

From the practical point of view, the essential fact is that the authors have found two dominant major genes that behave in accordance with expectation, provided that Classes '01', '1', and 'X' are grouped together as embracing the general genotypes **RR** and **Rr**. Thus, in the first and second generations from selfing selected resistant plants, either pure resistant families or families segregating three resistants to one susceptible against EA.1 were obtained. Table 1 lists those imported maizes from which pure resistant lines have been bred. The right-hand columns record the classes of reaction obtained by inoculating pure lines with Races EA.1 and EA.2 and the genes believed to be concerned.

TABLE 1. *The Juvenile Reaction of Maize Varieties to* Puccinia Polysora. *American Maizes from which pure Resistant Lines have been bred*

AFRO accession nos.	*Name or description at source*	*Source*	*Class of reaction to Rust Race EA.1*	*Class of reaction to Rust Race EA.2*	*Gene postulated*	*Remarks*
24	S.L.P.20–4A, once inbred at Ibadan, Nigeria (= Mex. 13 of W.A.M.R.U.)*	Mexico	01–1	01–1	**Rpp2**	Type for this gene
27	L II 123–2–1–8 × Coah.8–56A–4–2, once inbred at Ibadan (= Mex.22 of W.A.M.R.U.)	Mexico	1–X	1–X	(**Rpp2**)	
28	Hybrid Rocol, H–201	Colombia	01–1	01–1	(**Rpp2**)	
29 (*a*)	Variety, Colombia 2	Colombia	01	4	**Rpp1**	Type for this gene
(*b*)	Variety, Colombia 2	Colombia	01–1	01–1	(**Rpp2**)	
30	Variety, Eto	Colombia	01–1	01–1	(**Rpp2**)	
39	Ven.1–1–2–3	Colombia	01–1	01–1	(**Rpp2**)	
68	Br.106 ex Cuba	Trinidad	01	4	**Rpp1**	
71	Br.109 ex Cuba	Trinidad	1–X	1–X	(**Rpp2**)	
160	D.R.207 ex Dominican Republic	Trinidad	X	X	(? **Rpp2**)	
237	Rocol, H–201	Costa Rica	01	4	**Rpp1**	
250	Amarillo Coyotepe, ex Nicaragua	Costa Rica	01	4	**Rpp1**	

* West African Maize Rust Research Unit [6].

[1] These gene designations were adopted on the advice of Dr. M. M. Rhoades of the Maize Genetics Co-operation, University of Illinois, U.S.A. '**Rpp**' had already been used by the West African Maize Rust Research Unit [6].

Gene **Rpp1** was obtained originally from certain plants in the variety 'Colombia 2' (AFRO.29); and it is likely that this same gene has appeared also in AFRO.68, 237, and 250. That is, **Rpp1** has been obtained from Colombia, Cuba, Costa Rica, and Nicaragua. For **Rpp2** that obtained from AFRO.24 (from Mexico) the authors have regarded as the 'type'. It gives no differential reaction to the two rust races available to the authors. But while **Rpp2** from AFRO.24 tends to give the '01' reaction or mild '1's, the gene from AFRO.27, and some others, gives generally a severe '1' and sometimes 'X'. These differences might be due to different minor gene complements; and, unless new rust races become available and are found to react differentially to the pure lines derived from the different sources, it is considered unjustifiable to postulate more than the one major gene. Where, therefore, '**Rpp2**' has been enclosed in parentheses in Table 1, this doubt in identity is implied.

It will be observed that from different plants of 'Colombia 2' (AFRO. 29) each of the two genes was obtained. At first this was not recognized; but, as explained later, this failure had an important—and fortunate—effect on certain of the field breeding.

Resistant plants were found also in the thirty-four imported maizes listed below; but these have been insufficiently studied to identify the genes.

Colombia collection: three lines.
Trinidad collection: twenty-five lines, from Cuba, St. Croix, Martinique, Trinidad, Dominican Republic, Jamaica.
Costa Rica collection: six lines.

In all, therefore, resistance has been recognized in forty-five imported lines; the remainder were all susceptible in the samples tested.

At Muguga the authors (H. H. S. and A. K. H.) also made first crosses between selected resistant American plants and African susceptibles. Against EA.1 the F_1 families so raised were either wholly resistant (in accordance with expectation if the resistant parent were **RR**), or half resistant and half susceptible (resistant parent **Rr**). The F_2 families from selfing resistant plants in the F_1 all segregated 3:1 and F_3 families were either pure resistants or again segregated 3:1 [7].

Maintenance to Maturity of Resistance of the Plant

It was important to determine whether the juvenile resistance revealed in the Muguga tests would be maintained throughout the growth of the maize plant. Preliminary attempts to decide this were carried out in the glasshouses.

Seedling plants, whose juvenile behaviour had been determined, were transplanted and grown on in the glasshouses. Uredospores of Race EA.1 were dusted heavily on all leaves of the plants, which were then immediately enclosed in large polythene covers for 48 hours. This was repeated periodically until the plants tasselled. A second series was similarly treated, but, instead of being covered with polythene hoods, the plants were held in a small closed glasshouse and subjected to a continuous fine water spray, in an attempt to reproduce tropical conditions.

By each method control plants, which had reacted Class '4' as seedlings, developed large sori on most of the leaves formed up to tasselling. Resistant plants reacted in a manner generally similar to that in their seedling tests; plants showing juvenile reaction '01' gave mature reactions '01' or '1', while juvenile reaction '1' gave mature reaction '1'. Observations were continued usually until tassels and silks were dry, but no breakdown to class '4' was observed in any of the resistant plants.

The maize plant in the field can develop a variety of chlorotic and necrotic spots of uncertain cause and the diagnosis of lesions as definitely attributable to *Puccinia polysora* was impossible. Consequently the following modified system of classification was adopted in recording field experiments:

Class A: no sori of *P. polysora* detectable.
Class B: only small sori.
Class C: normal susceptible reaction of large sori.

Frequency of sori was not considered; the presence of even a single large sorus was sufficient to de-grade a plant to 'C', and of a single small sorus from 'A' to 'B'. Even with this simplified classification, field recording was not easy. In particular, Class 'B' was often difficult to differentiate from 'C'. However, the important Class was 'A', equivalent —provided adjacent control plants were heavily infected and accidental escape could be discounted—to the juvenile '01', or possibly, in view of the difficulties in field observation, mild Class '1'.

Field tests of a range of selected maizes were initiated at an E.A.A.F.R.O. station near Amani, Tanganyika, and at the breeding stations in Kenya, Uganda, and Tanganyika. Original seed from certain importations had been issued and grown in 1953; but the evidence obtained was doubtful and this first series was mainly valuable as providing experience in recording. Extensive and reliable trials were carried out in 1954 at four sites; results of testing families of known juvenile behaviour are summarized in Table 2.

The figures quoted are for the last of up to eight recordings made at weekly or fortnightly intervals from the first appearance of the disease on the control rows; except that, in the Amani trials, the figures are those of the inspection preceding the last. This last inspection was made when the plants were almost dry, and at this stage there appeared to have been much soral development on plants previously recorded as resistant. It is thus possible that resistance had broken down at Amani in the final stage of the life of the plant. No such breakdown, however, was observed at any other site.

The most important point that emerges is that generally resistance was maintained throughout growth at all of the widely separated sites; where juvenile tests had revealed the '01' or '1' reactions (against Race EA.1) in any family, this family showed some plants classed 'A' or 'B' in all the field tests. Because of the uncertainties of field recording it is scarcely worth while to attempt to derive much more from the figures than this outstanding fact. Nevertheless, for many families the recorded proportions of ('A'+'B'):'C' are not significantly different from expecta-

TABLE 2. *1954 Field Trials, against* Puccinia polysora, *of Maize Lines Bred at Muguga*

Origin	*No. of families tested*	*Ratio expected from Juvenile tests against EA.1 (A+B):C*	*Trials at Amani, Tanganyika**			*Trials at Nachingwea, Tanganyika (J. S. H.)*			*Trials at Kawanda, Uganda (B. J. T. B.)*		*Trials at Kilifi, Kenya (H. C. T.)*	
			Reactions			*Reactions*			*Reactions*		*Reactions*	
			A	*B*	*C*	*A*	*B*	*C*	*(A+B)*	*C*	*(A+B)*	*C*
1. *First selfs of American resistant plants*												
AFRO.24 Selfs . .	2	3:1	46	9	0	17	40	4	24	10	69	0
AFRO.27 Selfs . .	1	1:0	7	10	0	0	5	0	10	0	19	0
Same . . .	2	3:1	40	15	21	1	50	10	16	27	73	9
AFRO.28 Self . .	1	3:1	32	1	8	0	6	0	12	1	30	9
AFRO.29 Self . .	1	3:1	20	0	6	6	9	4	13	4	20	4
AFRO.30 Selfs . .	2	3:1	35	8	11	15	8	10	21	3	48	7
AFRO.31 Selfs . .	2	3:1	11	13	12	5	17	7	15	3	23	8
AFRO.32 Selfs . .	1	3:1	7	4	3	0	18	3	9	1	19	2
2. *First crosses of American resistant plants by susceptibles*												
AFRO.24 × Susceptible	1	1:0	1	35	7	0	10	0	15	9	17	10
Same . . .	1	1:1	16	3	27	0	22	28	12	8	30	16
AFRO.27 × Susceptible	2	1:1	3	10	37	0	14	33	14	23	6	11
AFRO.28 × Susceptible	1	1:1	7	4	15	0	15	14	7	6	..	..
AFRO.29 × Susceptible	2	1:1	29	3	27	24	13	37	18	14	50	22
AFRO.30 × Susceptible	3	1:1	48	6	54	0	53	47	23	25	52	52
AFRO.31 × Susceptible	1	1:1	4	9	28	0	10	29	3	12	20	9
Total control varieties .	..	0:1	0	0	181	Intermediate rows—all Class 'C'			all Class 'C'		all Class 'C'	

* Trials at Amani were planted and recorded by D. W. Gourlay.

tions based on juvenile tests. In particular, one family (from AFRO.27) believed homozygous was recorded 'A' and 'B' only at all sites. The most important deviations from expectation were:

(*a*) Among the selfed families there was a tendency for Class 'C' to be deficient; this was most marked in the two families from AFRO.24, which gave only Classes 'A' and 'B' at two sites, despite the glasshouse evidence that they were segregating. It is possible that some American maizes carried also a factor for field escape that was not recognizable in the juvenile tests.

(*b*) Among some of the crosses there was the opposite tendency for Class 'C' to exceed expectation. But, as already noted, **Rpp2** is not fully dominant; and a very severe Class '1' or 'X' of the juvenile tests might well be judged Class 'C' in the field. Thus one cross of AFRO.24, which at Muguga was resistant (although heterozygous), showed some Class 'C' plants at three of the four sites.

Similar trials were done at Amani, Nachingwea, and Kawanda in 1955, by which time pure-breeding lines had become available from Muguga. In general the 1954 evidence was confirmed (Table 3). Believed homozygous families carrying **Rpp2**, from selfings of AFRO.24, 28, and 30, all reacted 'A' or 'B' with none classed 'C'. Families from AFRO.27, supposed also to be carrying **Rpp2**, were, however, mostly classed 'C' at Amani (but 'A' and 'B' at Nachingwea): it has already been noted that AFRO.27 derivatives tended to react at Muguga as severe Class '1' and sometimes 'X', and so in the field might fall into Class 'C' in the observer's judgement. A more important exception, for which there is no explanation at present, was the appearance at Nachingwea of many Class 'B' plants in certain AFRO.29 derivatives that were carrying **Rpp1** and had reacted only '01' in juvenile tests. A similar degradation had been recorded in 1954 at Nachingwea. Class 'C', however, was absent from all these families.

In Group 2, Table 3, the pure-breeding F_3 families from crosses with susceptibles behaved in accordance with expectation; those derived from AFRO.24 were all classed 'A' and 'B'; and (at Nachingwea) the derivatives of AFRO.29 were classed 'A' only.

Field Breeding for Resistance

Imported seed was first distributed to breeding stations early in 1953; but the starting-point of most of the work was the distribution of first-generation material from Muguga at the end of 1953.

The agreed breeding programme was as follows: starting with selected resistant plants either of solely American origin or from the first crosses made at Muguga (i.e. from the first or second group of Table 2), to cross and back-cross to African maizes until sufficient conformity to type and vigour in the local environment was obtained, and thereafter to self to obtain pure-breeding lines. These lines could then be open-sibbed for bulk or handled by one of the recognized procedures to give an improved synthetic stock.

TABLE 3. *1955 Field Trials of Maize Lines bred at Muguga and believed to be Homozygous*

Origin	Gene believed to be carried	Reactions in juvenile tests against EA.1	Trials at Amani*				Trials at Nachingwea (J. S. H.)				Trials at Kawanda (B. J. T. B.)		
			No. of families	Reactions A	Reactions B	Reactions C	No. of families	Reactions A	Reactions B	Reactions C	No. of families	Reactions A and B	Reactions C
1. *Selfs of American resistant plants*													
S_2 from AFRO.24 . . .	**Rpp2**	01–1	3	66	0	0	4	136	18	0	5	174	0
S_1 and S_2 from AFRO.27 .	(**Rpp2**)	1–X	3	0	1	38	3	19	102	0	..	..	..
S_2 from AFRO.28 . . .	(**Rpp2**)	01–1	2	21	17	0	1	11	1	0	..	..	..
S_2 from AFRO.29 . . .	**Rpp1**	01	2	38	1	0	2	50	26	0	1	59	0
S_2 from AFRO.30 . . .	(**Rpp2**)	01–1	1	17	2	0	1	4	26	0	..	..	..
2. *Selfs of crosses of American resistant plants by susceptibles*													
F_3 from AFRO.24 × Susceptible	**Rpp2**	01–1	..	..	..	..	4	15	75	0	6	132	0
F_3 from AFRO.29 × Susceptible	**Rpp1**	01	..	..	..	..	2	32	0	0	2	26	0

* Trials at Amani were planted and recorded by D. L. Jennings.

From the earlier discussion of Table 2, it will be appreciated that selection for resistance during a rust epidemic presented no practical difficulty to the breeder. Preferably selection was made of Class 'A' plants, or, if 'A' was absent, the least affected of Class 'B'. The decision between classes 'B' and 'C', necessary for assessing genetic ratios, was here unimportant, because any doubtful 'B's were discarded. Indeed, in some of the work, selection was based simply on absence of uredosori from the leaves.

Breeding at Nachingwea, Tanganyika (J. S. H.)

Breeding at this station concentrated mainly on transferring resistance from AFRO.29 to the widely grown variety 'Katumbili' (mainly white dent). The starting-point was two Muguga crosses of AFRO.29 × 'Katumbili', 5314 and 5354. The lines developed from each were handled separately throughout.

In 1954 the resistant plants in 5314 and 5354 were back-crossed with the local 'Katumbili'. The families of this first back-crossed generation proved to be of satisfactory type and vigour; mean yields of the resistant plants were in fact three times as large as the mean of the adjacent diseased 'Katumbili' controls planted on the same day, and comparable with that of early-planted 'Katumbili' that had escaped serious rust infection. Consequently, although some plants were carried to a second back-crossed generation, the main effort was put into selfing the first back-crossed material, now carrying 75 per cent. of 'Katumbili' genes.

The growing of selected families was continued under irrigation without break during the normally rainless period (June to November). But during this period the rust epidemic died out and resistant plants could not be recognized; selection in this generation was therefore on agronomic characters only. This was true also of the second selfed generation, planted before the break of the rains in November 1954. Seed from this last generation, planted later in the rains of 1955, encountered heavy rust infection. This permitted typing for resistance, which showed proportions of families close to those expected, as follows:

	Number of families		
	Homozygous resistant	*Heterozygous resistant*	*Homozygous susceptible*
Actual	18	36	97
Expectation (1:2:5)	18·9	37·7	94·4

A number of the believed homozygous resistant lines were returned in 1956 to Muguga for confirmatory juvenile tests against both races of the fungus (Table 4).

Nine distinct derivatives of No. 5314 were all apparently pure[1] for

[1] Greenhouse space allowed of only ten plants per test (of which a few died); consequently the probability that a family, recorded all resistant, is homozygous is rather less than 95 per cent.

gene **Rpp1**, reacting '01' to Race EA.1 and '4' to EA.2. Of seven derivatives from 5354, one segregated and had evidently been mis-typed in the field; the remainder were all '01' or '1' to both races of the fungus. No. 5354, therefore, had carried gene **Rpp2** (or a gene indistinguishable from it).

TABLE 4. *Juvenile Tests of Nachingwea-bred Selected Second-selfed Lines. Muguga 1956*

Origin	*Gene*	*No. of families tested*	*Rust classes against Race EA.1*			*Rust classes against Race EA.2*	
			01	1	4	01–1	4
AFRO.5314 (AFRO.29 × 'Katumbili'), once back-crossed and twice selfed	**Rpp1**	9	75	0	0	0	79
AFRO.5354 (AFRO.29 × 'Katumbili'), once back-crossed and twice selfed	(**Rpp2**)	6	43	7	0	49	0
Same	(**Rpp2**)	1	5	1	1	8	2

Plants of the homozygous lines derived from 5314 and 5354 were top-crossed by local 'Katumbili' pollen during the 1955 dry season at Nachingwea, and the resulting progeny were grown in ear-rows in 1956 to compare the combining abilities of the parental lines, according to the method of Lonnquist [13]. The outstanding lines in each group were selected, and remnant seed of the parental lines bulked and planted under irrigation in the 1956 dry season, as nucleus stocks of three synthetics: (1) dent-seeded, ex No. 5314 (gene **Rpp1**); (2) flint-seeded, ex No. 5314 (**Rpp1**); (3) dent-seeded, ex No. 5354 (**Rpp2**). All these will be planted on a 5–10-acre scale in the 1957 season at Nachingwea. A number of single hybrid crosses between outstanding lines will also be made, to provide a comparison of the performance of such hybrids with that of the synthetics.

Until the breeding work was well advanced it was not known that gene **Rpp2** was present in the 5354 stock. While the main concentration had been on the AFRO.29 derivatives, hybridizing of AFRO.24 with local 'Katumbili' and back-crossing to it had been continued, in case this source of resistance proved necessary. Lines from this stock were selfed twice during 1956 and are therefore ready for typing in the field during the 1957 epidemic; the homozygous lines then identified will provide a second synthetic carrying **Rpp2**.

All the above four synthetics are white-seeded. Ordinarily, white maize is grown in Tanganyika; but there would be interest in a yellow-seeded maize for the export market, if a suitable stock could be developed. With this in mind two further synthetics were produced for testing on a 10-acre scale in 1957. For these, homozygous lines produced at Muguga were bulked; namely, F_3s from crosses of AFRO.29 with the local maize varieties 'Yellow Coast' and 'Durum', homozygous for **Rpp1** (and possibly also carrying **Rpp2**); and crosses of AFRO.24 with 'Yellow Coast', homozygous for **Rpp2**.

Breeding at Kenya Coast (H. C. T. and G. E. D.)

The Kenya programme was more widely based and at the start included eight susceptible varieties (six local and two imported) and twelve AFRO introductions in which resistance had been recognized in juvenile tests. Later many were eliminated and work was concentrated on transferring resistance from four introductions, AFRO.24, 27, 29, and 30.

Breeding started at Kilifi in 1953 with the crossing of the susceptible and resistant material noted above. The 1954 plantings included material of the second distribution from Muguga and consisted of twelve inbred lines and eleven crosses from Muguga in addition to twenty-one of the local Kilifi crosses of 1953. Upon this basis the recent work has been built in two distinct sections, namely, development of inbred lines from first crosses and repeated back-crossing to improve local adaptation.

In 1955 work was transferred to Kwale, a station a few miles inland, at 1,200 ft., where rainfall was higher and more reliable. Selfing and crossing were continued that year, and at the end of the season AFRO lines 24, 27, 29, and 30, crossed to local and imported varieties, were available both as S_2 inbred lines and twice back-crossed to local white maize. From the inbred material, selected progenies from plants resistant in the field were sent to Muguga for juvenile tests. Results of testing eighty-eight lines from seven crosses are recorded in Table 5.

TABLE 5. *Juvenile Tests of Second-selfed Kenya-bred Maize Lines. Muguga, 1956. Tests against Race EA.1 only*

Designation no. of line	*Parentage of original cross*	*No. of families tested*	*No. of families homozygous resistant*	*No. of families segregating*
A. *From crosses made in 1953 at Kilifi*				
Kilifi/2 . . .	AFRO.24 × 'Local White Cross'	17	11	6
Kilifi/3 . . .	AFRO.24 × 'Local White Cross'	14	7	7
Kilifi/17 . . .	AFRO.29 × '90 day'	24	9	15
B. *From crosses made at Muguga*				
AFRO.5318 . .	AFRO.24 × 'Muratha'	9*	4	4
AFRO.5338 . .	AFRO.24 × 'Yellow Coast'	4	2	2
AFRO.5314 . .	AFRO.29 × 'Katumbili'	13	5	8
AFRO.5315 (or 5317)†	AFRO.30 × 'N. Nyanza' (or 'Durum')	7	3	4

* One family was entirely susceptible.
† These two lines became confused and original susceptible parent now uncertain.

With one exception these tests confirmed the field observation and served to identify homozygous[1] resistant lines for use in the 1956 programme. It was likely that AFRO.24 and 30 derivatives would carry gene **Rpp2** and indeed they gave the expected '01' and '1' reaction to Race EA.1. On the other hand, AFRO.5314 (from AFRO.29) was likely to carry only **Rpp1**. This was confirmed by testing six progenies against Race EA.2; all gave the expected Class '4' reaction only.

[1] Probability less than 95 per cent.

The proportion of homozygous to heterozygous progenies among the derivatives of AFRO.29 was 14:23, which is not significantly different from the expected 1:2 ratio. The AFRO.24 and 30 derivatives showed 27:23, a deviation which may be attributed to the incomplete dominance of **Rpp2**. Field selection had been based on the absence of sori, and so tended to pick a disproportionate number of homozygotes from the field population.

In 1956 seventeen homozygous S_2 lines, derived from the original crosses of AFRO.24 and 29 to local and imported varieties, were put into a polycross plot, as the first stage in multiplying a resistant stock for use. In addition, a further thirty-two similar but still heterozygous lines were selfed again and selections will be tested prior to the sowings in 1957. Meanwhile the back-crossed material was given its third back-cross to local maize in 1956 and is now due to be selfed. When homozygous resistant lines are developed from these back-crosses, they will provide the basis of a new stock with greater local adaptation than that derived from the straight crosses.

Breeding at Kawanda, Uganda (J. D. J. and B. J. T. B.)

P. polysora has not been observed to cause severe losses to maize in Uganda. Nevertheless, it was decided to transfer resistance from the Muguga material to two locally important varieties, the high-yielding 'Muratha' and the quicker-maturing 'K8'. The initial crosses to 'K8' were stolen, so that this programme had to be begun again in 1955. The 'Muratha' programme has provided the basis of a rust-resistant synthetic variety in three years, but certain theoretical reservations have emerged from it.

Thirty-nine varieties were received from Muguga in 1953 and graded for resistance in the field at Kawanda. The results deviated from those in the glasshouses at Muguga in that AFRO.37 was classed as resistant and no resistance was detected in AFRO.29 and 30. In this initial work mis-typing may have occurred, but these discrepancies are recorded because of the importance of AFRO.29 in the subsequent work and because a further discrepancy involving AFRO.29 was noted at the end of it.

Starting from this material and twenty-five additional lines provided by Muguga, four generations were grown in 1954 and 1955. The first two were crossed or back-crossed to 'Muratha' (the second in the absence of a rust attack sufficient for efficient selection) and the last two were selfed to isolate homozygous resistant lines in 1956. Although no classification was possible in the second generation, the discrimination achieved in the other three was adequate for the purpose of a routine gene transference; and the ratios obtained between resistant and susceptible plants were broadly consistent with expectation.

In the early part of 1956 ninety-two lines of S_2 seed were subjected to the juvenile resistance test in the glasshouse at Kawanda. This was done partly to gain time in the off-season, but also because it was realized that a higher degree of discrimination was required in the final sort for the isolation of homozygous resistant lines. Methods were modelled on

those developed at Muguga; but the inoculum was bulked uredospores taken directly from plants in the field.

The results obtained were unexpected. Only six of the ninety-two families appeared to be homozygous for resistance factors and these were confined to S_2s derived from once back-crossed AFRO.24 × local crosses. The remaining families either segregated (51) or were fully susceptible (35).

Remnant seed from fifty-two of these families was planted in the field in the second season of 1956 with the results set out in Table 6, which includes the Kawanda glasshouse tests of the same families. The field test was clearly less exacting; whereas only six families had been classed as homozygous in the glasshouse, eleven survived rust-free in the field. Significantly, both tests failed to reveal any homozygous resistant families in Groups (3) and (4), derived from AFRO.29.

TABLE 6. *Tests of Second-selfed Kawanda-bred Maize Lines. Kawanda, 1956*

				Glasshouse tests			*Field tests*		
Group	*Genetic constitution*	*Gene*	*No. of families tested*	*Resistant*	*Segregating*	*Susceptible*	*Resistant*	*Segregating*	*Susceptible*
(1)	AFRO.24 (25%) × Local (75%)	**Rpp2**	24	6	18	0	9	15	0
(2)	AFRO.24 (12·5%) × Local (87·5%)	**Rpp2**	15	0	11	4	2	13	0
(3)	AFRO.29 (12·5%) × Local (87·5%)	**Rpp1**	8	0	5	3	0	8	0
(4)	AFRO.29 (12·5%) × Local (87·5%)	**(Rpp2)**	5	0	4	1	0	5	0

Note: certain lines in Group (2) were AFRO.24 × Yellow Coast × Muratha^2. All lines in groups (3) and (4) were AFRO.29 × Katumbili × Muratha^2. Otherwise the local element was Muratha.

An S_3 generation was raised from selected plants of the S_2 in the field test; and these families were typed, against Race EA.1, in the glasshouses at Muguga. The results recorded in Table 7 indicate a number of homozygous resistant families in both lines—6 out of 17 among AFRO.24 derivatives and 7 out of 17 among AFRO.29 derivatives.

TABLE 7. *Juvenile Tests of Third-selfed Kawanda-bred Maize Lines. Muguga, 1956*

			Muguga tests against Race EA.1			
Group	*Origin*	*Gene*	*No. of families tested*	*No. of families resistant*	*No. of families segregating*	*No. of families susceptible*
(1)	AFRO.24	**Rpp2**	17	6	9	2
(2)	AFRO.29 (ex 5314)	**Rpp1**	9	3	6	0
(3)	AFRO.29 (ex 5354)	**(Rpp2)**	8	4	4	0

No explanation of the anomalous results can be offered at this stage. There is a suggestion that the tests at Kawanda do not conform with those at Muguga; the opportunity for studying this apparent discrepancy

will be taken in 1957, when seed of known reaction at Muguga will be grown at Kawanda.

Discussion

The work here described has clearly afforded promise of practical control of *Puccinia polysora* in East Africa. Intensive studies in the glasshouses at Muguga, in co-operation with field breeding in endemic areas, have produced a wide range of resistant, locally adapted maize types within little over four years from the first appearance of the disease. This outcome has resulted mainly from the early recognition and isolation of genes for resistance in Central American maizes.

Field breeding advanced most rapidly at Nachingwea where irrigation and a favourable climate permit the raising of three crops of maize in one year. In 1957 multiplication was in progress there of a range of rust-resistant stocks, white- and yellow-seeded, flint- and dent-seeded, carrying one or other of the two resistance genes. In Kenya and Uganda progress is only slightly less advanced, although work at the latter site has encountered difficulties not yet resolved.

At first sight, therefore, control appears to be assured as soon as the improved stocks can be issued to cultivators. But success will depend on the continued stability of the fungus; and a clear warning exists in experience with the rusts of small cereals, where the development of new physiologic races of the fungi has tended to overtake the work of the plant breeders. There is also the even more cogent warning in the fact that a second physiologic race of *P. polysora*, EA.2, had been recognized within three years of the appearance of the species in East Africa.

So long as EA.1 remains the only, or the predominant, race in the field, maize stocks carrying genes **Rpp1** or **Rpp2** are likely to maintain effective resistance. If EA.2 becomes established in the field, **Rpp1** will cease to be useful, but **Rpp2** (and the genes provisionally identified with it) will continue to provide resistance. That new physiologic races may emerge capable of overcoming the resistance provided by **Rpp2** must remain a constant threat. With this in mind, breeding of pure resistant maize lines has been undertaken at Muguga, from as many as possible of the sources already listed. If new races of *P. polysora* appear, these lines may provide not only differential hosts for identifying the races, but also resistance genes that can be incorporated in the local maize varieties.

This work has concentrated on the protoplasmic characters that cause maize to give the hypersensitive type of reaction to the rust fungus. Indications that some maize varieties may possess an ability to escape severe damage from a rust attack have been referred to. Of the nature of this character nothing is known; and seedling tests in the glasshouses have afforded no indication. If with maize, as with wheat, the emergence of new physiologic races of the rust should overtake the production of hypersensitive types, this ability to escape, possibly effective against all races, may assume great importance. But, until *P. polysora* has shown an ability to produce rapidly a range of different physiologic races, the positive resistance afforded by the genes so far studied appears to justify maximum exploitation.

FIG. 1. Class '01' × 2·4

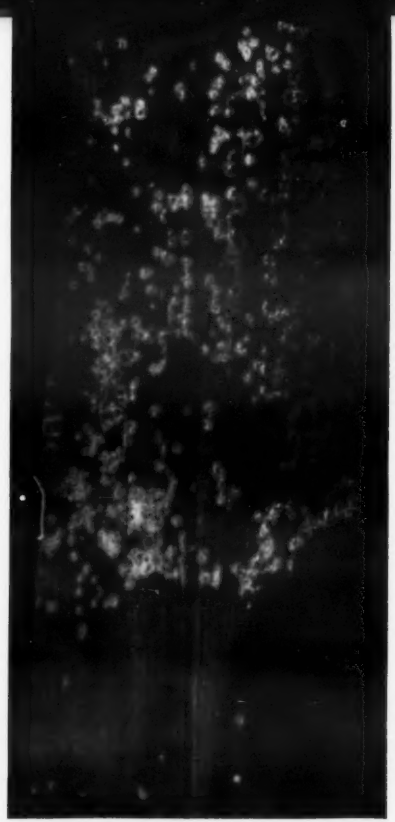

FIG. 2. Class '1+' × 2·4

FIG. 3. Class '4' × 2·4

FIGS. 1–3. Rust reactions on leaves of maize seedlings inoculated with *Puccinia polysora* Underw. in the glasshouse

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(*Received 15 March 1957*)

VARIATION OF SKIN THICKNESS IN DAIRY CATTLE

U. G. PATEL[1] AND D. W. ANDERSON

(*A.R.C. Animal Breeding Research Organisation, Edinburgh*)

Summary

A study of skin-fold thickness of 313 animals of varying ages is presented. The mean skin thickness corrected to an age of 2 years varied from 0·224 in. on the elbow, for a group of mixed breeding, to 0·449 in. at the end of the last rib, for Friesians. The intra-class correlations of skin thicknesses at five different places on the same animal was 0·65. Differences between skin thickness on the different body parts were highly significant.

There was marked association of the skin thickness with age and with weight, the relationship being curvilinear in both cases.

Friesians had slightly thicker skin than Ayrshires or the other breeds studied.

Skin thickness on the point of the last rib was relatively more variable than on the other body parts. There are indications of genetic variation in skin thickness on all parts.

SKIN thickness of cattle has some economic interest deriving from the weight and value of hides as well as a physiological significance not yet fully appreciated. It may well play a part, as Bonsma [1] believes, in determining how an animal reacts to temperature and humidity. Dowling [2] has reported on some sources of variation in skin thickness under Australian conditions, and this led to observations on the twin-cattle herd maintained under dairying conditions by the Animal Breeding Research Organisation in Scotland. The factors considered in this report are the effect of age and weight on skin thickness, the variation due to place of measurement on the body, and breed differences. The material also offered an opportunity for studying the genetic variability of the character.

Material and Method

The animals studied consisted mainly of one-egg (MZ) and two-egg (DZ) twins, pairs of half sisters (HZ), and pairs of unrelated heifers (U). There were also some pairs of full sisters and also single animals. The method of identification of twins, the area of collection, and the system of management and feeding have been described by Donald [3]. The approximate breeding and number of pairs in each breed are given in Table 1.

In all, there were 313 animals. The classification of breeds is approximate, some high grades and three-quarter-breds being included amongst their respective breeds. The cross-breds are mostly of Ayrshire with Friesian. Age varied from 5 weeks to 6 years.

For the sake of accuracy in measurement, Dowling [2] prefers the

[1] Now of Institute of Agriculture, Anand, India. The work reported in this paper was done during the tenure of a post-graduate research studentship at the Department of Genetics of the University of Edinburgh.

[Empire Journ. of Exper. Agric., Vol. 26, No. 101, 1958.]

biopsy technique after anaesthetizing the skin. This could not be used on the present material so skin-fold measurements without anaesthesia were taken.

The micrometer used had a spring-and-ratchet arrangement slipping at constant pressure. On the jaws of the instrument round disks of about $\frac{3}{4}$-in. diameter were fixed. This contrivance helped in measuring approximately the same amount of the fold every time, and also reduced the penetrating effect of the narrow edges of the jaws.

The measurements were taken at five different places on the left side of the animal. The sites selected were (1) the neck about a hand span above the shoulder towards the head, (2) the side of the brisket towards the axilla, (3) the point of the elbow, (4) the end of the last rib, and (5) the area about a hand span above the point of the hock joint. These areas are referred to as neck, brisket, elbow, rib, and hock.

TABLE 1. *Numbers and Types of Pairs of Animals measured*

Breed	*MZ*	*DZ*	*HZ*	*FS*	*U*	*Singles*
Ayrshire . . .	26	16	20	..	26	2
Friesian . . .	16	10	4	1	..	2
Shorthorn . . .	4	3	2	..	..	..
Guernsey . . .	1	1	..	..	..	..
Cross-breds . . .	8	7	3	5	..	3
Total . . .	55	37	29	6	26	7

MZ: one-egg twin pairs; DZ: two-egg twin pairs; HZ: half-sister (contemporary) pairs; FS: full-sister (same sire, one-egg twin mothers) pairs; U: unrelated (contemporary) pairs.

All animals were housed for the winter when measured. The members of a twin pair were measured together. The areas of measurement were exposed by clipping the hair as closely as possible. Some animals were nervous, especially when the brisket fold was measured. All measurements were done by the same person single-handed, except in the case of the hock when a second person helped by holding the skin-fold. They were repeated at an interval of a day or two to test the accuracy of the operator. Although the records were made to the nearest 0·001 in., the figures were rounded off to 0·01 in. for analysis.

Results

Although great care was taken to obtain accurate measurements, and the environment was controlled as far as possible, there are many factors such as subcutaneous fat, turgidity of the skin, temperature of the animal and barn, straining of muscles, nervous temperament, health and pose of the animal, which might have affected the results. Nevertheless, the study should give some indication of the variation of the skin thickness in dairy breeds.

Repeatability

The correlations between the first and second measurements for the 313 animals were high. They averaged 0·87 for the five sites, the lowest being 0·77 for the brisket and the highest 0·97 for the rib.

Variation in Thickness of Skin from Site to Site

Of the five sites studied, the thickest skin was found on the rib and the thinnest on the elbow (Table 2); the difference is marked, the former being about 1·8 times as thick as the latter. The difference between the neck and the hock skin was very small and not significant; that between

TABLE 2. *Means (M) and Standard Deviations (SD) in inches and Coefficients of Variation (CV) for Age-corrected Data on Skin-fold Thickness*

		Neck			*Hock*			*Brisket*		
Breed	*No.*	*M*	*SD*	*CV*	*M*	*SD*	*CV*	*M*	*SD*	*CV*
Ayrshire	178	0·293	0·029	10·0	0·309	0·029	9·0	0·253	0·033	13·0
Friesian	64	0·307	0·029	9·0	0·304	0·029	9·0	0·254	0·030	12·0
Crossbred	71	0·300	0·033	11·0	0·295	0·029	10·0	0·247	0·028	11·0
		Elbow			*Rib*			*Mean of five sites*		
	No.	*M*	*SD*	*CV*	*M*	*SD*	*CV*	*M*	*SD*	*CV*
Ayrshire	178	0·229	0·028	12·0	0·430	0·058	13·0	0·303	0·026	9·0
Friesian	64	0·237	0·026	11·0	0·449	0·058	13·0	0·310	0·025	8·0
Crossbred	71	0·224	0·029	13·0	0·420	0·047	11·0	0·297	0·022	7·0

brisket and elbow, though not very large, is significant at the $P = 0·01$ level.

Although, therefore, there was some variation from site to site on the same animals, individuals nevertheless varied as a whole towards thickness or thinness of skin. Correlations between pairs of sites were all large and significant and the overall intra-class correlation (within breeds) for sites on the same animal was 0·65.

Age and Thickness of Skin

In order to study this relationship, the cattle were classified into age groups with an interval of 8 weeks. Since, however, the different breeds were far from being equally or uniformly distributed by age, the breed distinction was ignored. The mean thickness of skin for animals in each age group was plotted against age. The resulting figure is not given, but resembles Fig. 1 (see p. 22) which shows the weight-thickness relationship. There was a steady increase in thickness up to the age of 97 to 104 weeks, after which there was a small decrease. Elbow skin, the thinnest throughout, was about 0·14 in. at about 4–20 weeks and reached a maximum at 2 years of 0·23 in. Rib skin, in the same period, changed from 0·18 in. to about 0·43 in. The skin at the remaining sites was intermediate in thickness at all ages. The values for brisket, elbow, neck, and hock all showed similar curves; the rib skin

increased in thickness markedly more than the others. This was possibly due in part to deposition of fatty tissue.

Analysis of variance of neck skin thickness showed highly significant differences between age groups and it is assumed that other sites would do likewise. Dowling [2] concluded that 'under good nutritive conditions, the skin thickness did not vary to any appreciable extent with age'. He appears to have based this statement on data from too few ages.

As there is undoubtedly a marked effect of age on skin thickness, it is desirable to allow for this before comparing breeds. Therefore age correction factors were derived in order to transform all thicknesses to an equivalent thickness at the age of 97 to 104 weeks—the age of maximum thickness. In this procedure, all animals above 176 weeks were included in a single group as their number was small. Three sets of factors were derived, the first for the neck and the hock, the second for the elbow and the brisket, and the third for the rib. These factors expressed thickness at 97–104 weeks of age as a percentage of the thicknesses at other ages.

Breed Differences

There were 178 animals of Ayrshire or Ayrshire type, 64 of Friesian or Friesian type, and the remaining 71 were Shorthorns, Guernseys, or cross-breds (collectively called cross-breds).

Table 2 presents the mean, standard deviation, and coefficient of variation of the age-corrected data. Friesians were shown to have slightly thicker skin than the Ayrshires, except on the hock. Ayrshires had thicker skin than the cross-breds on all parts except the neck. Friesians had thicker skin than the cross-breds on all parts. The mean skin thickness on all parts was significantly greater in Friesians than in Ayrshires or cross-breds, which did not differ significantly from each other. All breed differences were small.

Weight and Thickness

The raw data were also classified according to live-weight into 50-lb. class intervals and the mean thickness of the skin of the animals in each class was calculated and plotted against the mid-class value for weight. As shown in Fig. 1, skin thickness is clearly associated with the weight of the animal. It increased markedly up to a weight of 600 to 650 lb., after which the curves became flat. Regressions of thickness on weight were accordingly worked out for animals up to 650 lb. weight and for those above that weight. These regressions were then used for correcting skin thickness to a weight of 400 lb. for the first group and of 942 lb. for the second group. The regression coefficients for the older group were small and not significant. For both groups combined, the weight-corrected mean thickness for the Friesians was greater than for the Ayrshires or the cross-breds, and the outcome of the breed comparison was generally the same as that obtained from the age-corrected data.

The reduction in the coefficient of variation was slightly greater when age was held constant than when the weight effect was eliminated, but this might be accounted for by the difference in the technique of correction. Since the correlation between age-corrected rib skin thickness and

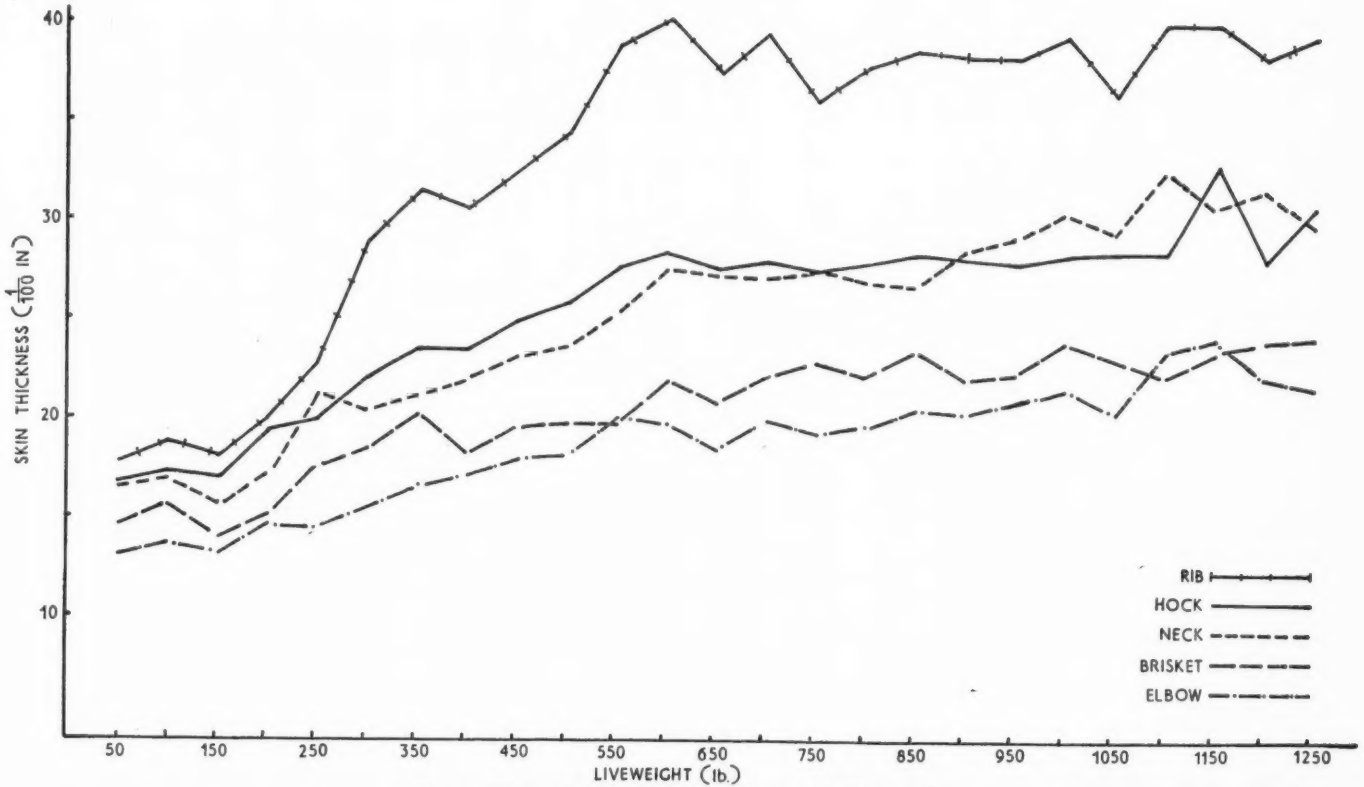

FIG. 1. Change in Mean Skin Thickness with Liveweight.

weight was negligible, it would seem that there is nothing to be gained beyond a single correction either for weight or for age.

Genetic Variation

No reports on the importance of heredity as a source of variation in skin thickness have been found. Apart from breed differences, the present data, coming as they do from twins, permit some intra-breed genetic variation to be demonstrated. For this purpose, the age-corrected data were reclassified and the variance analysed according to type of pair.

Since the results for the several body sites are sufficiently well repre-

TABLE 3. *Analysis of Variance of Mean Skin Thickness (unit = 0·01 in.) at Five Body Sites*

Pairs		*Mean square*		
Type	*Number*	*Between pairs*	*Within pairs*	*Total*
MZ	55	87	21	53
DZ	37	71	23	45
HZ	29	71	43	56
U	26	68	53	61

sented by those for the mean of them all, only the latter are shown in Table 3.

If there was a perceptible amount of genetic variation in skin thickness, the intra-pair variance should have increased with decreasing genetic relationship while the total variance for each type of pair remained more or less constant. As Table 3 shows, this is, in fact, what was found.

There were minor exceptions among the results of analysis for individual body sites in so far as, for brisket and elbow measurements, DZ pairs had a smaller intra-pair mean square than MZ pairs. This need occasion no surprise, for it has been observed before [4] that DZ pairs tend to behave more like MZ than HZ pairs, probably as a result of their twin origin.

FIG. 1. Change in Mean Skin Thickness with Liveweight.

Discussion

These observations confirm Dowling's [2] report of breed differences in skin thickness. Direct comparison of data collected under different conditions has perhaps only limited value. The twins here described were in their winter coats, and, as far as those in milk were concerned, at different stages of lactation. If skin thickness, as measured, includes a variable amount of fatty tissue, there may well be changes with season, level of nutrition, and health, that are not comprehended in the present report. Apart from fatty deposits, there may be changes in thickness due to variation in the cellular activity of the skin itself. By studying individual animals at a series of ages, more precision could be obtained on such questions. The considerations, however, should not affect the comparison of the different classes of twin or other type of pair from which it is fairly clear that genetic differences in skin thickness occur.

Which parts of the skin are responsible for this, and what physiological significance it may have, remain to be determined.

Acknowledgements. The authors wish to thank Dr. H. P. Donald and Dr. St. C. S. Taylor for their help in connexion with this work.

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(*Received 6 May 1957*)

FERTILIZER EXPERIMENTS IN CYPRUS: II. CEREALS

P. A. LOIZIDES

(*Department of Agriculture, Nicosia, Cyprus*)

Summary

The results of experiments with nitrogen and phosphorus fertilizers on wheat and barley are reported and discussed.

The yield of wheat and barley was consistently raised by dressings of nitrogen fertilizers even after a fallow, in spite of the considerable accumulation of nitrate- and ammonia-nitrogen in the soil during the fallow year.

The response to phosphorus fertilizer was far less consistent than that of nitrogen.

Late applications of nitrogen were generally more effective than early ones, but usually the difference was small.

In two experiments with barley, the yield with sodium nitrate was higher than with ammonium sulphate or Nitrochalk, but the differences were not significant.

The problem of soil organic matter and nitrogen is discussed.

LITTLEJOHN [1] has summarized the results of two long-term fertilizer experiments with continuous wheat in Cyprus, which showed that this crop needed nitrogen as well as phosphorus fertilizers. In those experiments the quantitative effects of the two kinds of fertilizer could not be separated. Moreover, since cereals in Cyprus are generally grown after fallow or a summer crop, the results of the experiments might not be generally valid, in view of the accumulation of mineral nitrogen in the soil in the fallow year [2]. A number of experiments have accordingly been carried out in various localities with wheat and barley grown after a bare fallow.

Experimental Details

A description of the climate and soils of Cyprus was given in the first paper in this series [3].

In all experiments described in this paper durum wheats and four-rowed barley were employed. These are the types exclusively grown in Cyprus. Only grain yields are given, since the response of straw to fertilizer treatment was almost invariably similar to that of grain. The fertilizer was applied broadcast in all experiments.

All the experiments, except the long-term experiments described on p. 27, were of factorial design.

Effect of Late Application of Nitrogen and Phosphorus Fertilizers on the Yield and Composition of Wheat and Barley

In these experiments one half of the nitrogen fertilizer in each treatment was applied as ammonium sulphate in the seed-bed in December, and the other half as Nitrochalk as a top-dressing in February. All the phosphorus fertilizer was applied as 16 per cent. superphosphate in the seed-bed in December.

[Empire Journ. of Exper. Agric., Vol. 26, No. 101, 1958.]

Table 1 gives the results of two experiments on wheat. Experiment 1 was on a rendzina clay soil at Papho. Experiment 2 was on a shallow calcareous terra rossa clay soil at Margo.

TABLE 1. *Effect of Nitrogen and Phosphorus Fertilizers on Yield of Wheat grown after Bare Fallow (cwt. grain per acre)*

P *treatments: cwt.* P_2O_5 *per acre*	*Mean yields for all* N *levels*		N *treatments: cwt.* N *per acre*	*Mean yields for all* P *levels*	
	Expt. 1	*Expt. 2*		*Expt. 1*	*Expt. 2*
Nil (P_0)	10·8	9·7	Nil (N_0)	10·5	11·2
0·12 (P_1)	11·5	12·3	0·12 (N_1)	10·9	12·0
0·24 (P_2)	11·4	12·4	0·24 (N_2)	11·1	14·2
0·36 (P_3)	10·8	15·1	0·36 (N_3)	12·4	13·1
S.E. (15 D.F.)	±0·50	±0·93	S.E. (15 D.F.)	±0·50	±0·93

The linear effect of nitrogen ($3N_3+N_2-N_1-3N_0$) was significant (at $P = 0·05$) in the first experiment and nearly so in the second, in which N_2-N_0 was significant. The effect of phosphorus was marked in the second experiment but not in the first. The NP interaction was very small in both experiments and is not given in this table.

Table 2 gives the results of two experiments on barley.

Experiment 1 was on a highly calcareous shallow reddish-brown clay loam soil at Deftera. Experiment 2 was on a shallow calcareous terra rossa clay soil at Papho.

TABLE 2. *Effect of Nitrogen and Phosphorus Fertilizers on Yield of Barley grown after Bare Fallow (cwt. grain per acre)*

P *treatments: cwt.* P_2O_5 *per acre*	*Mean yields for all* N *levels*		N *treatments: cwt.* N *per acre*	*Mean yields for all* P *levels*	
	Expt. 1	*Expt. 2*		*Expt. 1*	*Expt. 2*
Nil (P_0)	11·4	8·0	Nil	8·8	6·1
0·18 (P_1)	11·8	8·9	0·18	12·0	7·6
0·36 (P_2)	11·9	7·7	0·36	13·3	10·7
S.E. (16 D.F.)	±0·96	±0·56	S.E. (16 D.F.)	±0·96	±0·56

In both experiments a marked and highly significant effect of N was obtained, but P had no effect. Again the NP interaction was negligible and is not given here.

These four experiments show that even after a fallow there was a marked response to nitrogen. The effect of phosphorus was variable, presumably because of the residual effect of previous dressings.

Further experiments and demonstrations lead to the same conclusion as regards the effect of nitrogen. Some of these experiments, dealing with type of nitrogen fertilizer and time of application are described later in this paper. Here mention must be made of the results of four long-term experiments in which wheat or barley was grown continuously after fallow or after vetches cut green. Individually they are little more

than demonstrations, since there is no replication at any given centre so that the significance of a given yield-difference in any one year cannot be assessed. However, the nitrogen dressings were associated with increased yields consistently every year at every centre, although the magnitude of the increase varied considerably. When the experiments at the four centres are treated as replications the effect of nitrogen can be calculated to be highly significant. The results, summarized in Table 3, are for the plots receiving superphosphate only. The experiments include plots without superphosphate, but up to now the effect of this fertilizer has been insignificant.

TABLE 3. *Effect of Nitrogen Fertilizers on the Yield of Wheat in various Rotations (cwt. grain per acre. Means for 1950–6)*

Soil and locality	*Wheat continuous*		*Wheat after fallow*		*Wheat after* Viciasativa *cut for hay*	
	N 0·18 *cwt./acre*	N 0·36 *cwt./acre*	*No* N	N 0·18 *cwt./acre*	*No* N	N. *mean of* 0·18 *and* 0·36 *cwt./acre*
1. Calcareous alluvial clay. Nicosia	5·1	5·5	4·9	6·5	4·1	6·2
2. Shallow eroded calcareous terra rossa clay. Lefkonico . .	4·7	5·7	4·9	7·4	4·3	8·1
3. Deep calcareous loam. Lyssi .	5·0	5·6	6·5	8·2	6·2	8·7
4. Calcareous terra rossa clay. Kokkinotrimithia						
Barley 1950–3 . . .	6·9	7·4	4·2	11·2	5·8	10·8
Wheat 1954–6 . . .	6·5	8·4	9·6	6·2	6·9	8·4

The table shows clearly the effect of nitrogen. The yields may seem low, but are actually well above the average for wheat in Cyprus, which does not exceed 5 cwt. of grain per acre. These experiments are all located in the central plain under an average annual rainfall of 14 in., and the period 1950–6 includes a year of almost complete crop failure because of drought. There are years, however, when the yield of wheat with nitrogen fertilizers exceeds 15 cwt. per acre. An interesting observation is that in these, as well as in the other experiments described here, nitrogen fertilizers almost invariably hastened the maturity of the crop, as judged by the loss of green colour, by a week or more. It is generally considered that nitrogen delays maturity, but this is probably true only where excess is applied, especially on land deficient in phosphorus. On land deficient in nitrogen, moderate additions of this nutrient, where the supply of phosphorus is adequate, appear to have the opposite effect.

It is also interesting to note that the yield of continuous wheat with nitrogen fertilizers is considerable, if account is taken of local conditions. Where no fertilizers are used the yield of continuous wheat in Cyprus is extremely small even under irrigation [1]. It appears that nitrogen and phosphorus deficiencies limit the production of cereals to an even greater extent than shortage of moisture.

A number of other experiments in addition to these show that the effect of superphosphate is not consistent. Some of them will be reported in a subsequent paper in this series, on the effect of various types of phosphorus fertilizer on wheat. In all, out of fifteen experiments, in only seven was a significant response to superphosphate obtained. This probably indicates not so much the presence of adequate reserves of soil phosphorus, as the residual effect of earlier regular dressings of superphosphate.

In one experiment at Morphou the effect of regular dressings of superphosphate was followed up for five years. This is actually the experiment reported in Table 5 (p. 29), mainly designed to test the effect of nitrogen fertilizer and time of its application. The results with superphosphate, shown in Table 4, are the means for three levels of nitrogen.

TABLE 4. *Effect of Regular Dressings of Superphosphate on the Yield of Wheat (cwt. grain per acre)*

Superphosphate: cwt. P_2O_5 *per acre*	*1947–8*	*1948–9*	*1949–50*	*1950–1*	*1951–2*
0·18	9·1	13·5	8·8	No	8·7
0·36	9·7	15·1	9·1	results	10·9
0·54	10·9	15·4	9·6		8·7
S.E. (8 D.F.)	±0·29	±0·56	±0·24		±0·53

In the third year, dressings up to 0·54 cwt. P_2O_5 per acre continued to give significantly better results than 0·18 cwt. In the fifth year, 0·36 cwt. gave better results than 0·18 cwt., but 0·54 cwt. was no more effective than the lowest dressing. This anomaly cannot be explained.

Plant analysis. All the analytical results reported here have been obtained on wheat before ear emergence in the middle of March when the plant was about three months old. Determinations of total nitrogen and phosphorus have been carried out on the whole plant cut 1 in. above the ground. Data are available for the two annual experiments (Table 1) and for two years of the four long-term experiments (Table 3).

It has been found that the nitrogen content in experiment 1 (Table 1) was 3·02 per cent. of the dry matter of the plant for the plots receiving no nitrogen fertilizer, and 3·11 for the plots receiving the triple dressing. The corresponding figures for experiment 2 are 2·51 and 2·90. In the four experiments of Table 3 the nitrogen content of the plants receiving no nitrogen fertilizer varied from 2·36 to 2·85 per cent. and in those receiving nitrogen fertilizer from 2·55 to 2·80 per cent. It appears that a nitrogen content of less than 3·0 per cent. before ear-emergence is indicative of nitrogen deficiency.

The average phosphorus content in experiment 1 (Table 1) was 0·291 per cent. in the plants receiving no superphosphate and 0·288 in those receiving superphosphate. In experiment 2 the corresponding figures were 0·201 and 0·271 per cent. Thus in this experiment, in which the response to phosphorus was large, not only was the phosphorus

content of the plants much smaller than in experiment 1, but also the dressing of superphosphate raised this content considerably. In this experiment the dressing of ammonium sulphate had a large effect on the phosphorus content of the plants. Thus, in the P_3 plots this content was: without N, 0·236 per cent.; with N_3, 0·294 per cent. There is further evidence from other experiments and demonstrations that dressings of ammonium sulphate may favour the uptake of added phosphorus, but the effect is not consistent.

In the four experiments of Table 3 the phosphorus content varied from 0·225 to 0·260 per cent. in the plants grown without superphosphate, and from 0·243 to 0·289 in the plants grown with it. In these experiments superphosphate had no appreciable effect on yield. It appears therefore that a threshold value for phosphorus content must lie below these figures, probably at or slightly above 0·200 per cent. of the dry matter of the plant. This threshold value may, however, not be applicable to crops having an abundant supply of moisture.

Effect of Time of Application of Nitrogen Fertilizers

Some experiments have been carried out to test the effect of time of application. In 1947 a factorial split-plot experiment with continuous wheat began at the Morphou farm of the Department of Agriculture, on a calcareous alluvial clay loam soil. The whole-plot treatments were combinations of three levels of nitrogen and three of phosphorus and the half-plot treatments were two different times of application of nitrogen: an early application (E), in which all nitrogen was applied in the seed-bed in December as ammonium sulphate, and a split application (S), in which one-quarter was applied with the seed as ammonium sulphate and three-quarters two months later, in February, as Nitrochalk. The results are given in Table 5.

TABLE 5. *Effect of Amount and Time of Application of Nitrogen Fertilizers on Yield of Wheat Grown Continuously (cwt. grain per acre. Means for three levels of* P)

N *applications* (*cwt./acre*)	N_1 *0·12*		N_2 *0·24*		N_3 *0·36*		*S.E.* (*17 D.F.*)
	E	*S*	*E*	*S*	*E*	*S*	
1947–8 .	9·2	9·4	8·8	10·6	9·2	11·0	±0·34
1948–9 .	13·7	13·7	14·5	14·2	15·1	16·0	±0·40
1949–50 .	9·0	8·1	9·2	9·2	9·2	10·4	±0·37
1950–1 .	No results						
1951–2 .	8·8	9·3	8·8	10·0	9·7	10·1	±0·56

The highest yields were obtained with the highest rate of application of nitrogen, but the differences are mostly small and not significant. Split applications were more effective, but only at the second and third nitrogen levels, and not every year. Similar results were obtained for straw yields, except that in 1949 the yield was significantly higher where all the nitrogen was applied at the time of sowing. This experiment,

which received an irrigation in March each year, was finally abandoned owing to heavy wild-oats infestation which it proved impossible to eradicate.

The effect of time of application was further investigated in an annual experiment with non-irrigated wheat after fallow, on a calcareous alluvial clay soil at Tricomo. Three levels of application at three different times were compared. The times of application were: all nitrogen applied in the seed-bed in December (E); one half applied with the seed and the other half as a top-dressing in February (S); and all nitrogen applied as a top-dressing in February (L). The fertilizer applied with the seed was ammonium sulphate and the top-dressing was Nitrochalk. Basal dressing: 2·5 cwt. superphosphate per acre. Table 6 shows the results.

TABLE 6. *Effect of Time of Application and of Amount of Nitrogen Fertilizer on Yield of Wheat after Fallow*

Treatment N	*Yield of grain* (*cwt. per acre*)	
Nil	17·2	S.E. (16 D.F.) ±0·52
0·18 E	18·6	
0·18 S	17·7	
0·18 L	18·5	
0·36 E	18·7	±0·90
0·36 S	20·6	
0·36 L	19·0	

The results are remarkable for the high yields obtained without irrigation. The response to nitrogen was small, but the mean yield obtained with the higher level of nitrogen is significantly higher than that of the control. Variations in the time of application, however, had no significant effect.

Two experiments with barley have been carried out on the relative effect of the types of nitrogen fertilizers applied at three different levels and at three different times. The results, given in Table 7, show that 0·33 cwt. of N per acre were more effective than the lower levels. In one experiment, late applications proved significantly more effective than early ones, with split applications intermediate. In the other experiment, late applications did not lead to significantly better results. The yields with sodium nitrate were higher than those with the other two fertilizers, but the mean differences were not significant, although in experiment 1 the difference between the yields with sodium nitrate and with ammonium sulphate at the higher level of application was significant at the $P = 0{\cdot}05$ level.

In experiment 1 the December–January rainfall was 8·21 in.; in experiment 2, 11·45 in. The difference of about 3 in. is probably not sufficient to explain the marked differences observed in the effect of time of application. On the whole, early applications proved less effective than late ones in most of the experiments described here, but the differences in this effect from one experiment to another, or, as in Table 4, from one year to another, cannot be adequately explained by differences

in the amount of rainfall during the period preceding top-dressing. Thus in the experiment described in Table 4 the December–January rainfall was: 1947–8, 6·2 in.; 1948–9, 7·2 in.; 1949–50, 10·2 in.; 1951–2, 6·1 in.; while the difference in favour of late applications was significant only in 1947–8 and to a lesser extent in 1949–50.

TABLE 7. *Effect of three Types of Nitrogen Fertilizers and of Time of Application on the Yield of Barley (cwt. grain per acre)*

	Experiment 1 Shallow reddish clay loam. Deftera				*Experiment 2 Eroded calcareous terra rossa clay. Papho*			
	Ammonium sulphate	*Nitro-chalk*	*Sodium nitrate*	*Mean*	*Ammonium sulphate*	*Nitro-chalk*	*Sodium nitrate*	*Mean*
0·11 cwt. N	9·9	7·4	7·9	8·4	9·5	10·6	10·8	10·3
0·22 ,, N	9·5	11·5	11·5	10·8	12·0	15·9	16·8	14·7
0·33 ,, N	12·1	13·6	16·7	14·1	18·0	16·2	18·7	17·6
E	11·1	12·0	11·0	11·4	11·0	10·0	11·9	11·0
S	9·6	8·8	11·4	9·9	14·0	15·1	16·7	15·9
L	10·8	11·7	13·6	12·0	14·6	17·7	17·7	17·0
Mean	10·5	10·8	12·0	11·1	13·2	14·3	15·4	14·6
S.E. (13 D.F.)	Body of table ±1·35 Means ±0·78				Body of table ±1·90 Means ±1·10			

E: all fertilizers applied in the seed-bed in December.
S: one-half applied at sowing, the other as top-dressing in February.
L: All fertilizers applied as top-dressing.

Effect of Fertilizers on Quality of Wheat

The effect of fertilizers on the quality of wheat grain was not studied in these experiments, but Ramadan has reported [4] on the effect in the experiments described by Littlejohn [1]. The effect of nitrogen fertilizer was mainly to raise the percentage of vitreous (flinty) grains as compared with starchy grains. The percentage of crude protein was also raised by nitrogen dressings, but the effect was not marked except in the animal-manure plots, where the crude-protein content of the grain was 15·4 per cent. as against 12·7 per cent. in the grain from the continuous-wheat, unmanured plots. The effect of superphosphate was to reduce the proportion of flinty grain and the crude-protein content of the grain. The effect of fertilizers on quality is complicated by the marked increases in yield brought about by nitrogen fertilizer in the presence of super-phosphate. In Cyprus the last dressing of nitrogen is given before ear-emergence, i.e. three to four months before harvest, and its effect may be expected to be much more marked on the yield than on the quality of grain.

The Problem of Soil Nitrogen

The accumulation of nitrates and, to a lesser extent, of ammonia after a fallow is a well-known phenomenon. Loizides [2] has demonstrated this accumulation in Cyprus soils. His results also show that the beneficial effect of fallow cannot be due to storage of moisture. These conclusions have been confirmed by further determinations of moisture

and mineral nitrogen carried out over a period of three years on the unmanured wheat/fallow plots in experiment 3 (Table 3). This soil was chosen because it is fairly uniform and also because of the ease with which samples down to 5 or 6 ft. can be taken in a few minutes with a jarret auger. In two years out of the three there was no difference in the moisture content between the fallow and stubble plots at sowing time in December, but in one there was a difference exceeding 2 in. for the entire 5-ft. layer. In the same month the mineral-nitrogen content in the first foot was 22–26 parts per million after fallow and 7–12 parts per million on stubble. In March there were 5–10 p.p.m. mineral nitrogen in the first foot after fallow, while the deeper layers always contained substantial amounts of mineral nitrogen in all months, rarely falling below 5 p.p.m.

Thus, the first foot alone, after fallow, contained at sowing time about 0·8 cwt. of mineral nitrogen per acre, while the amount needed for a 5-cwt. wheat crop, including 10 cwt. of straw, probably does not exceed 0·25 cwt. nitrogen, even if the nitrogen in the roots is allowed for. Yet wheat responds to dressings of 0·18 cwt. of nitrogen per acre or even less. Much of the mineral nitrogen is leached from the first foot during the rainy season, but enough remains in the first 2 ft. alone to cover the requirements of a bigger crop than 5 cwt. of grain per acre. The response to nitrogen fertilizer thus indicates not an absolute shortage of available nitrogen but rather a low concentration which must be raised in order that satisfactory amounts may be taken up by the crop.

The soil sampled contained 0·7–0·9 per cent. organic matter and around 400 p.p.m. *total* nitrogen in the top foot. This corresponds to about 1,400 lb. nitrogen per acre. The crop removes 18–20 lb., some of which comes from the lower layers. Leaching removes large amounts. If only one-half of the 22–26 p.p.m. of mineral nitrogen in the top-soil is so removed, the loss will amount to over 40 lb. per acre. Recent work [5] has also indicated the probability of aerobic denitrification. Taking all losses into account, all nitrogen could disappear from the first foot in forty to sixty years, i.e. twenty to thirty crops. Yet production under the wheat/fallow rotation, although low, appears to be capable of going on for ever. The soils of Cyprus have been farmed since early historical times and must presumably have reached equilibrium between the increased rate of removal of nitrogen under agriculture and the rate of addition. Even badly eroded soils, which must have lost all the nitrogen originally present in the top-soil, contain a stable amount of organic matter of 0·7–1 per cent. and of nitrogen 0·04–0·06 per cent.

Where does the nitrogen come from? Rain probably adds 3–5 lb. nitrogen per acre. The contribution of leguminous plants is low because of the low phosphorus status of the soil and the destruction of legumes as well as of other weeds by cultivation during the fallow year. One must turn to other sources. It is interesting to note that recent work by Jones [6] indicates that considerable increases in the total nitrogen content of the soil may occur even during the dry season in the Sudan Gezira. This suggests the presence of non-symbiotic nitrogen-fixing bacteria adapted to an extremely dry environment. In this connexion Jones

mentions the earlier work by Greene, who has found in the Sudan Gezira strains of Azotobacter capable of fixing nitrogen in a dry soil.

In spite of its scientific interest and practical importance, the question of nitrogen balance, as well as the related question of organic-matter balance, in semi-arid and arid countries has not been adequately studied, but it should amply repay further investigation.

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(*Received 21 March 1957*)

NOTE ON THE INFLUENCE OF DEPTH OF SOIL COVERING THE PARENT TUBER ON THE DEVELOPMENT AND YIELD OF THE POTATO PLANT

J. D. IVINS AND V. J. MONTAGUE

(*University of Nottingham School of Agriculture*)

Summary

The depth of soil overlying the seed tuber at planting time was found to affect, in particular, the number of tubers produced by potato plants. Shallow coverings led to an increase in the average numbers of tubers per plant, with consequent general reduction in size. Possible explanations based on environmental effects are given and the possibility of the application of this phenomenon to ware and to seed production is discussed.

IN the years 1955 and 1956 trials with potatoes were laid down to determine the possible factors causing the wide variation in yield and tuber numbers per plant found to exist among individual plants in commercial crops. In the previous two years some 3,000 random plants had been sampled in healthy crops of several varieties, and yields and tuber numbers per plant were found to vary between 16 and 270 per cent. of the mean values per plant. The existence of strains with varying yield potential within the variety could not be established, for selections based on the performance of the parent plant during 1953 and grown in the following year showed no significant differences in yield or tuber numbers. The effects of known virus diseases were not believed to have any influence on these results. Consequently factors of crop management were investigated.

In a given crop depth of planting may vary, particularly when seed potatoes are planted by mechanical means. The trials here reported refer to the depth of soil overlying the seed tuber rather than to the depth of planting, for in practice ridges may be harrowed down at varying stages after planting and rebuilt again during the process of earthing up, thus rendering the figures for initial depth of planting of no consequence.

Experimental

The trials were carried out at Sutton Bonington on a light loam overlying valley gravel. A general manuring of 14 tons of farmyard manure and 8 cwt. of a compound fertilizer ($N:12/P_2O_5:12/K_2O:15$ per cent.) was applied. Seed tubers, graded between $1\frac{3}{4}$ and 2 in., of the varieties King Edward and Ulster Prince were planted in late April in 1/500th-acre plots, in rows 28 in. apart with the setts 15 in. apart in the rows. Randomized block layouts were used, with fourfold replication. Planting was done by hand dibber in pre-formed ridges and cultivations were restricted to the removal of weeds by hand. The differential treatments consisted in leaving a covering of soil of a specified depth over the seed

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tuber at planting time. Crops were lifted by hand when mature (end September), and the produce of each plant was counted, graded, and weighed.

In 1955 the summer was dry and hot, with an August rainfall of 0·29 in. and total rainfall May to September of 9·65 in. In 1956, after a dry May (0·51 in.), the summer was abnormally wet, with 4·19 in. of rain in August and 10·64 in. for May–September inclusive.

Results

TABLE 1. *Influence of Depth of Soil-Cover on Total Yields and Number of Tubers per Plant*

Variety	*King Edward*						*Ulster Prince*			
Year	*1955*			*1956*			*1955*		*1956*	
Depth of soil cover (in.) . . .	1	4	7	1	4	7	1	6	1	4
Average tuber number per plant .	27·0	17·5	15·1	18·7	15·3	12·6	15·2	10·8	7·9	6·4
Yield per acre (tons)	11·1	11·1	9·6	10·7	10·7	9·2	15·6	14·3	12·6	13·7

TABLE 2. *Influence of Depth of Soil-Cover on Size Grades of Tubers, 1956*

Variety: King Edward

Depth of soil cover (in.)	*Yield of tubers (tons/acre)*					*Average number of tubers per plant*				
	Over 2¼″	*2¼″–1¾″*	*1¾″–1¼″*	*Below 1¼″*	*Total*	*Over 2¼″*	*2¼″–1¼″*	*1¾″–1¼″*	*Below 1¼″*	*Total*
1	1·4	5·3	3·2	0·8	10·7	0·7	5·3	6·8	5·9	18·7
4	2·4	5·4	2·4	0·5	10·7	1·3	5·6	5·0	3·4	15·3
7	2·1	4·7	2·1	0·3	9·2	1·2	4·7	4·3	2·4	12·6

Variety: Ulster Prince

	Yield of tubers (tons/acre)				*Average number of tubers per plant*			
	Over 2¼″	*2¼″–1¼″*	*Below 1¼″*	*Total*	*Over 2¼″*	*2¼″–1¼″*	*Below 1¼″*	*Total*
1	5·4	7·0	0·2	12·6	1·5	5·1	1·3	7·9
4	8·4	5·1	0·2	13·7	2·2	3·6	0·6	6·4

Invariably, leaving a shallow cover of soil on the parent tuber led to an increase in the average number of tubers produced per plant. These differences were significant (at $P = 0·05$) throughout, for all depths of soil covering. Deeper soil coverings generally led to reduced total yields but in no case was the difference significant (at $P = 0·05$). As might be expected deeper soil coverings resulted in delayed emergence and this in all probability accounted for the reduction in yield. Even though the early leaves of plants resulting from shallow planted tubers in these

and other trials were damaged by frost in 1956 the advantages of early emergence were apparent throughout in terms of yield.

Tubers planted with a shallow soil covering gave rise to plants with slightly higher numbers of stems per plant compared with those resulting from deeper plantings, but these differences were not found to be significant.

Discussion

It is held, for example by Clark [1], Fellows [2], and Krijthe [3], that tuber-set takes place, within a matter of a few weeks, early in the life of the potato plant and that the final differences in size of tubers are due to unequal rate of growth, rather than to differences in their age. Temperature appears to be an important factor governing tuber set and formation [4, 5] and a possible explanation of increased tuber numbers resulting from a shallow depth of soil over the parent tuber may lie in the considerably greater fluctuations of soil temperature which occur nearer the surface of the soil. In addition, or alternatively, fluctuating moisture content of the soil near the surface may have some effect. Of more remote possibility is the effect of day-length. Werner [5] has shown day-length to be a factor of considerable importance in tuber formation and it is conceivable that owing to varying times of emergence, the plants arising from different depths of planting may have passed through critical times of tuber-set at different times and hence different day-lengths. The advantages of early emergence are, however, more usually attributed to a longer growing season.

The varieties King Edward and Ulster Prince provide two great contrasts. The former popular maincrop is notorious for the production of a relatively large number of small tubers which the ware grower frequently finds unsaleable, while the latter early variety in the main presents problems to the seed grower by the production of a small number of large tubers. The size of 'seed', and spacing, are well known to influence the size-composition of a crop of potatoes (e.g. Bates [6]) but it would also appear possible to influence the size-composition by manipulation of the depth of soil overlying the seed tuber fairly early in the life of the potato crop. In practice this would be determined by the time and severity of harrowing-down the ridges after planting, at the same time paying due regard to the control of weeds by this treatment. Unless careful earthing up is later practised, a shallow soil covering of 1 in. depth results in a high proportion of greened tubers, which, however, may not be of great consequence to the seed grower.

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(*Received 21 February 1957*)

THE BREEDING OF SORGHUM IN EAST AFRICA. II. THE BREEDING OF WEEVIL-RESISTANT VARIETIES

H. DOGGETT

(*Agricultural Department, Tanganyika*)

Summary

New strains of short-term sorghum with weevil-resistant grains are being developed by crosses between the variety B.C.27 from the Belgian Congo and the Tanganyika variety Wiru. Yield figures and results of weevil-resistance tests are given: the latter show that selection for a thick corneous endosperm shell in the grain has been successfully used in breeding for weevil resistance.

THE first objective of the sorghum work at Ukiriguru is to produce high-yielding, early-maturing sorghum varieties, having grains which will be sufficiently weevil-resistant to remain sound in the peasants' food stores for at least one year: and it is also important that the grains should yield a palatable, white flour when prepared by local methods.

In the previous paper [1], it was shown that there is a sufficiently close association between the thickness of the outer corneous endosperm shell of the grain, and weevil resistance, for this character to be of use in breeding for weevil resistance.

In the present paper an account of the breeding of early-maturing sorghums with weevil-resistant grains is given, together with yield and storage-test data for new strains produced.

Breeding

The sorghum varieties indigenous to Tanganyika are all long-term (5–7 months) and mostly tall (8 ft. high, or taller). Those most prized by the people have grains that are white throughout, with largely corneous endosperms: such grains keep well in store, and yield a palatable flour of good appearance.

Many short-term varieties (3–4 months) were introduced, but few of them yielded consistently well under Tanganyika conditions. Those that did yield well had soft, mealy grains, of very poor keeping quality, and giving a relatively unpalatable flour of poor appearance.

An examination of the material showed that there was little prospect of selecting short-term strains out of the indigenous long-term varieties: and selection for white, corneous, weevil-resistant grains within the introduced short-term varieties seemed equally unpromising. A hybridization programme was therefore started. Several parents have been used, to give a wide range of variability, but this paper is concerned with the progeny from only one pair of parents, with which the most progress has been made.

Methods. A modification of the hot-water technique of Stephens and Quinby [2] was used for emasculating the heads. One or two days before the onset of flowering, the heads were surrounded by a sleeve containing

[Empire Journ. of Exper. Agric., Vol. 26, No. 101, 1958.]

hot water which was maintained at 46° C. for 10 minutes. The emasculated heads were pollinated for several days in succession. This method yields a high proportion of hybrid seed. Plants were self-pollinated by bagging the heads.

Parents. Seed from bulks maintained by mass selection was used, as no selfed lines were available at that time.

B.C.27, used as female parent in the crosses, is a variety taking about 3½ months from germination to harvest; it is about 5 ft. tall, and has yielded consistently well at Ukiriguru for 12 years. The grain is white with a dark nucellar layer, and the endosperm is almost wholly mealy and soft. This variety was originally selected at Ukiriguru from 27 U.T., obtained from the Belgian Congo about 1938.

Wiru is an indigenous variety taking 5 to 6 months from germination to harvest; it is some 10 ft. tall, and the yield is rather light. The grain is white throughout, and the endosperm is largely or wholly corneous.

Crosses. The F_1 generation from the B.C.27 × Wiru cross consisted of plants as tall as, and as late maturing as those of the Wiru parent, and the grains resembled those of the B.C.27, having a very thin corneous endosperm shell, except that the seed coat colour was light brown.

The most striking feature of the F_2 generation was the poverty of the plants with very corneous grains, the great majority being weak, with poor panicles, and many had tight glumes.

Selections taken from the F_2 generation for the combination of thick corneous endosperm shell, earliness of maturity, and panicle size, were selfed and reselected for several generations, eventually yielding the strain SUK 1 (SUK = Sorghum Ukiriguru), which is referred to in greater detail below.

The F_1 generation of the B.C.27 × Wiru cross was backcrossed to the B.C.27 parent. All corneous shell layers in the grains of the B_1 generation were thin. Plants with corneous grains in the next generation of this B.C.27 (2) × Wiru backcross were more vigorous than those from the F_2 of the first cross, the panicles were larger, and few had tight glumes. Selfing and reselection for several generations yielded two promising strains, 42 B and 36 D, which are mentioned below.

The Behaviour of the Thick Corneous Endosperm Shell in these Crosses

The F_2 generation of the B.C.27 × Wiru cross was analysed for thickness of corneous endosperm shell, measurements being taken along the diameter of the grain below the style scar. Table 1 shows this analysis, with grain colours.

There was a large excess of pure white grains with thick corneous shells (8 units and thicker), with very few coloured grains having thick shells (181 white grains with thick shells to 22 coloured). Other data collected suggested independent segregation of length of maturity and thick corneous endosperm shell.

The distribution of the thickness of corneous shell in the parents, and the F_1 and F_2 generations of the B.C.27 × Wiru cross, is shown in Fig. 1.

The B_1 of the B.C.27 (2) × Wiru backcross gave 220 plants with brown grains to 206 plants with white grains but dark nucellar layers. It was

TABLE 1. *Classification of F_2 Plants of B.C.27 × Wiru Cross for Thickness of Corneous Endosperm Shell, and Colour of Grains (numbers of grains)*

Thickness class (unit = $\frac{1}{12}$ mm.)	*Plants Brown grains*	*Plants White grains with dark nucellar layer*	*Plants Grains white throughout*	*Total Plants*
0,1	226	33	16	275
2,3	262	52	5	319
4,5	222	49	26	297
6,7	41	26	40	107
8,9	6	2	66	74
10,11	1	2	27	30
12,13*	9	2	88	99
Total	767	166	268	1,201

* Wholly corneous grains were counted as having a layer thickness of 13.

not possible to analyse in detail the selfed progenies from this backcross: all plants with a good corneous layer in the grain were identified, and 118 B_1 plants threw such grains in the next generation, while 296 did not. (The seed of twelve B_1 plants did not germinate in the field.)

The New Strains Obtained

Material line-bred from the B.C.27 × Wiru cross was generally disappointing, the combination of good corneous grain and large panicle proving impossible to obtain. One line was developed as a variety, SUK 1. It matures in 3½ months, and is about 4–5 ft. high; the plants are vigorous and relatively free from leaf diseases. The grain is white, with a thick corneous endosperm shell, and free-threshing; the flour is of good quality, but the size of the panicle is disappointing, and this variety is very susceptible to grain smut (*Sphacelotheca sorghii*).

SUK 1 appeared promising for yield in the 1953–4 season: it yielded at the rate of 2,070 lb./acre of grain on a half-acre bulk at Lubaga,[1] and 930 lb./acre on a 2-acre bulk at Ukiriguru. The 1954–5 season results were disappointing, the rainfall early in the season being very low. Yields were 400 lb./acre on 30 acres at Ukiriguru, and 350 lb./acre on 85 acres at Lubaga. Yield on a trial plot at Dodoma[2] was 1,440 lb./acre; two trials at Ilonga[3] gave 1,680 and 1,750 lb./acre.

Yields in district plot[4] trials in the Ukiriguru area are shown in Table 2.

Two lines have been developed from the B.C.27 (2) × Wiru back-

[1] Lubaga is a sub-station of Ukiriguru, about 80 miles to the south.

[2] Dodoma is the principal town of the Central Province of Tanganyika.

[3] Ilonga is an experiment station near Kilosa, in the Eastern Province of Tanganyika.

[4] District plots were originally started for cotton variety trials by J. E. Peat of the E.C.G.C. and some are used for the sorghum trials. The plots are cultivated by Africans, using their ordinary hand methods, but the general standard of ridging, timeliness of planting, and weeding, is rather above that of the surrounding peasant fields. Butulwa is 5 miles west of Lubaga on a different soil type and Mwanangwa is 20 miles south of Ukiriguru.

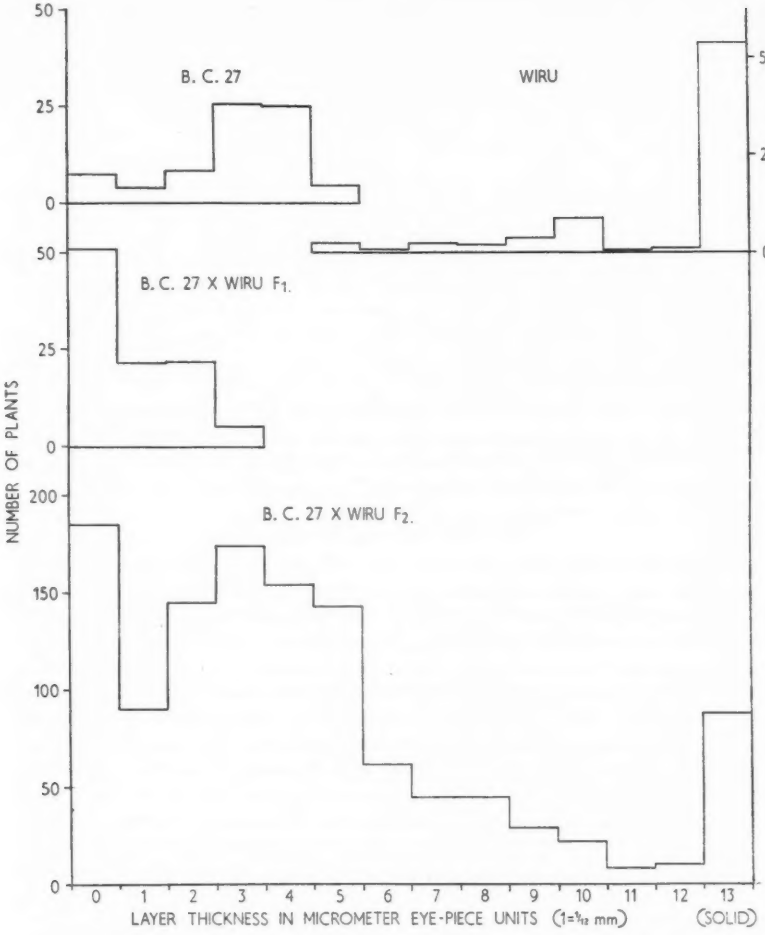

FIG. 1. Distribution of Thickness of Corneous Endosperm Shell in B.C.27 × Wiru Cross

cross: 36 D and 42 B. Both mature in around 4 months, and have larger panicles than the SUK 1. (Panicle size is an important character in the eyes of the local people.) 36 D is the more vigorous vegetatively, but has a larger grain, with a rather lower proportion of corneous material: instead of being distributed as a shell, the corneous material tends to be accumulated in the upper part of the endosperm, often with an appreciable mealy layer between it and the embryo. The 42 B has a more open panicle, and the grain has a well-distributed, thick corneous shell.

TABLE 2. *Sorghum Variety Trials; Yields of Grain in lb./acre*

Plot	*Butulwa*		*Mwanangwa*		*Lubaga*	
Variety	*1953–4*	*1954–5*	*1953–4*	*1954–5*	*1953–4*	*1954–5*
Bukura Mahemba*	565	295	1,040	750	830	400
Dobbs† . .	890	1,010	480	1,060	745	490
B.C.27 . .	505	410	380	1,045	1,455	95
SUK 1 . .	585	595	710	980	1,580	260
L.S.D. at P = 0·05	110	100	110	240	250	75

* A local, brown-grained sorghum rather widely grown, especially where birds are prevalent. It matures in about 5 months.

† A short-term sorghum from Kenya, with a soft brown grain, but giving consistently good yields. It matures in just over 4 months.

Yield figures are available for only one season, and are shown in Table 3.

TABLE 3. *Yields of Varieties in lb. of Grain per acre in District Plots Trials 1955–6*

Variety	*District Plot*			*Mean*
	Butulwa	*Mwanangwa*	*Lubaga*	
Bukura Mahemba .	380	980	1,950	1,100
Dobbs . . .	1,380	1,600	2,640	1,870
B.C.27 . . .	620	1,370	2,750	1,580
SUK 1 . . .	290	820	1,710	940
36 D . . .	450	1,040	2,450	1,300
42 B . . .	840	860	2,040	1,250
L.S.D. at P = 0·05 .	130	230	205	. .

Figures over a number of seasons will be needed, but the strains 36 D and 42 B seem to yield better than SUK 1. They are probably as productive as the local Bukura Mahemba variety, but clearly there is much room for improvement before the yield level of Dobbs is reached.

Weevil Resistance of the New Strains

It remains to demonstrate that these strains produced from the B.C.27 × Wiru cross, and backcross, and selected for a high proportion of corneous material in the endosperm, are in fact weevil-resistant.

Bulks of the two parent varieties, the progenies SUK 1, 36 D, and 42 B, and of the American variety Oklahoma 44/14 (Dwarf Kaffir 44/14) were planted at the same time in the same field. This last variety was planted for comparison, since it is well known in several sorghum-growing countries. The 36 D and 42 B bulks were of less highly selected seed (as stocks were very limited), so the figures for corneous shell, and presumably weevil resistance, may be below those of the best lines.

After harvest, the usual observations [1] on thickness of corneous shell, and grain volume, were made. Shell thickness for all varieties is the mean of measurements of 100 grains, along two diameters in

longitudinal section, to allow for the uneven distribution in 36 D: percentage of corneous material was calculated as in the previous paper. Two parallel sets of storage tests were run, the first using the net-bag method as described in the first paper, the second using 8 lb. bulks.

Weevil-resistant Tests by the Net-bag Method

Results of this test, and grain measurements, are shown in Table 4.

TABLE 4. *Weevil-resistance Tests. 100 grain samples, nine replications (14 September 1955 to 28 January 1956)*

Variety	*Mean percentage damaged grain*	*Thickness of corneous shell in endosperm (unit = $\frac{1}{12}$ mm.)*	*Volume of 1,000 grains (c.c.)*	*Estimated percentage of corneous material in endosperm*
SUK 1 . . .	18·0	10·05	16·0	90
42 B . . .	22·7	9·48	14·6	90
Wiru . . .	22·8	10·96	13·8	95
36 D . . .	34·1	7·68	17·1	80
Oklahoma . .	40·1	3·88	18·8	50
B.C.27 . . .	47·9	1·97	19·0	25
L.S.D. at P = 0·05 .	9·0	0·67	0·4	..

Curves for the rates of damage are shown in Fig. 2.

The behaviour of these varieties in this test is in line with the results of previous tests [1], the varieties Wiru, SUK 1, and 42 B with the thickest corneous endosperm shells having succumbed to weevil attack more slowly than the remainder.

The Bulk Tests

Six 8-lb. samples of each variety, sewn up in unbleached calico bags, were stacked on planks in the form of a vertical Latin square. The square was surrounded by an edging of 8-lb. bags of B.C.27, but there was not enough grain to supply an edging at the front and back of the square. One object of the B.C.27 edging was to obtain an estimate of the weevil movement between bags. Between 23 and 27 September 1955, 100 weevils (*Calandra oryzeae*) were placed in each of the bags under test, but not into the B.C.27 bags forming the edging. The stack was then left undisturbed until 30 January 1956, when all the bags were placed in drums, and well fumigated with 'Kiloptera': no live weevils were found after treatment. The weevils were sieved out of the grain, and their numbers estimated by weighing. No insects other than weevil were found. The grain in the bags was then separated into sound and damaged, by floating in water: separation was repeated until it was as complete as possible. After drying, the sound grain was weighed, and the loss determined by subtraction from 8 lb. (3,630 gm.). The damaged grain was also weighed, as a check. Table 5 shows the arrangement of the trial. The figures in brackets show the numbers of weevils recovered

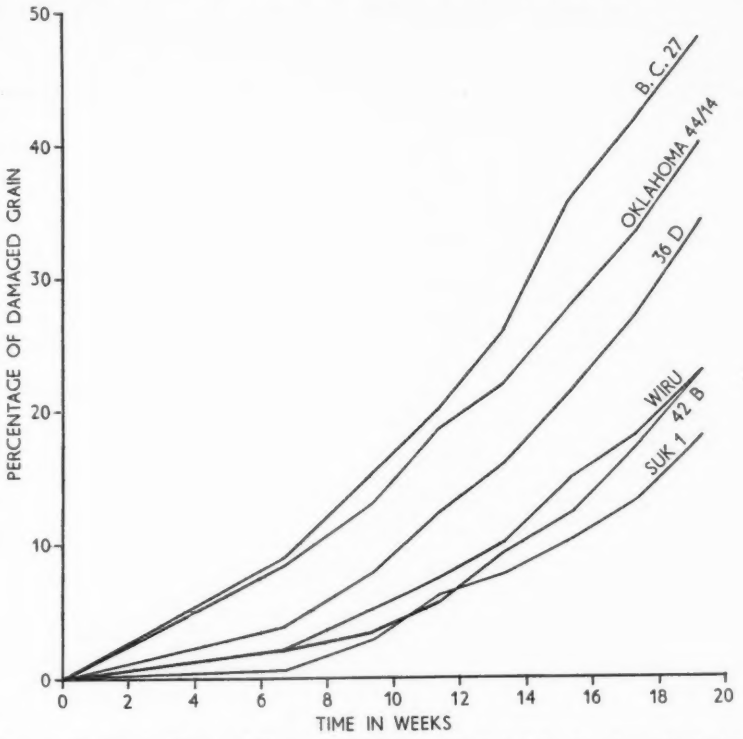

FIG. 2. Curves for Rates of Damage in Net-bag Tests for the Sorghum Varieties in Table IV

(thousands), and the other figures show the weight, in grammes, of the sound grain recovered.

The last column, the loss in weight divided by the number of weevils, was calculated as a check: Wiru, and perhaps Oklahoma 44/14, may have had handling losses, or the separation of sound grain may have been less complete, as their ratios are high: but on the whole this trial may be regarded as satisfactory, if somewhat crude.

The weevil population in the B.C.27 edging shows that considerable weevil movement occurred: the test is still a very severe one, although less so than the net-bag tests. With a large bulk of grain, and weevil infestation starting from a few individuals who find their way into it, the rate of damage may be expected to be slower than in this test.

Comparison of the Bulk and Net-bag Tests

The results obtained from the two types of test are rather similar: in the bulk tests, the differences between varieties have fanned out more than in the net-bag tests, the percentage losses of the good-storing

TABLE 5. *Layout and Individual Plot Data of Bulk Test of Grain for Weevil Resistance*

(Edging all B.C.27) TOP

(6·1)	(4·2)	(6·7)	(4·2)	(12·5)	(9·7)	(4·9)	(6·8)
(6·7)	B.C.27 (12·6) 1,965	42 B (3·8) 3,287	36 D (11·4) 2,545	Wiru (0·5) 3,395	SUK 1 (3·0) 3,260	Okl.44/14 (4·8) 2,895	(10·5)
(8·3)	Wiru (0·2) 3,477	36 D (6·5) 2,718	SUK 1 (3·2) 3,247	Okl.44/14 (6·7) 2,665	B.C.27 (9·7) 2,350	42 B (4·4) 3,205	(3·1)
(3·7)	42 B (4·2) 3,300	Wiru (0·6) 3,505	Okl.44/14 (4·1) 2,810	SUK 1 (0·3) 3,490	36 D (7·4) 2,828	B.C.27 (8·0) 2,245	(15·6)
(10·9)	SUK 1 (1·8) 3,365	Okl.44/14 (3·6) 2,860	42 B (3·0) 3,245	B.C.27 (11·0) 2,455	Wiru (0·6) 3,540	36 D (4·8) 3,000	(6·6)
(4·3)	36 D (8·6) 2,732	SUK 1 (3·2) 3,220	B.C.27 (13·4) 2,395	42 B (2·3) 3,400	Okl.44/14 (3·7) 2,852	Wiru (1·0) 3,430	(8·8)
(14·3)	Okl.44/14 (7·3) 2,515	B.C.27 (13·8) 2,008	Wiru (1·2) 3,427	36 D (7·8) 2,615	42 B (1·0) 3,422	SUK 1 (4·7) 3,180	(13·0)
(5·9)	(7·8)	(3·0)	(4·1)	(12·0)	(3·8)	(12·0)	(3·6)

BOTTOM On wooden planks

In the analysis, the mean square for vertical columns is not significant ($F = 1·33$); that for the horizontal rows is significant at $P = 0·05$ ($F = 3·16$). Varietal differences are highly significant. Table 6 summarizes the results.

varieties being markedly lower. This was to be expected, as the intensity of weevil attack on 100 grains buried in a weevily grain bulk must be much greater than in an 8-lb. bulk which started with only 100 weevils

TABLE 6. *Results of Bulk Test. Period of Test 4 months (23/27 September 1955 to 30 January 1956)*

Variety	*Total weight of sound grain recovered (gm.)*	*Loss: 21,780 (6 × 3,630) minus sound grain*	*Loss (damaged grain) %*	*Damaged grain actually recovered*	*Wastage*	*Total number of weevils (thousands)*	*Ratio: loss in gm.: number of weevils*
Wiru	20,775	1,005	4·6	865	140	4·1	0·25
42 B	19,860	1,920	8·8	1,120	800	18·7	0·10
SUK 1	19,760	2,020	9·3	1,105	915	16·2	0·12
Okl.44/14	16,595	5,185	23·8	3,075	2,110	30·2	0·17
36 D	16,440	5,340	24·5	2,755	2,585	46·5	0·11
B.C.27	14,420	8,360	38·4	4,800	8,560	68·5	0·12
L.S.D. at P = 0·05	835	..	3·8	..	..	..	..

in it, and which was presumably not subject to invasion by weevils from surrounding bags until some time had elapsed.

The differences between varieties at the $P = 0{\cdot}05$ level are not radically different in the two tests. The grouping is very similar, the three varieties with very corneous grains, Wiru, SUK 1, and 42 B, are decidedly more weevil-resistant than B.C.27, with 36 D and Oklahoma 44/14 intermediate. More comparative tests of the bulk and net-bag methods would be desirable, but at present it would seem that the net-bag test is a useful one when only small quantities of grain are available.

Discussion

Breeding weevil-resistant, short-term sorghum varieties by selecting for grains with a thick corneous endosperm shell has met with fair success. The new strains SUK 1 and 42 B have both shown a much higher degree of weevil resistance than the B.C.27 parent: they do not seem to be as weevil-resistant as the Wiru parent, but the proportion of corneous material in their grains is rather lower. The strain 36 D is disappointing: it is better than B.C.27, but has shown a lower weevil resistance than expected. Its behaviour in the storage tests is not sufficiently bad to suggest that selection for a corneous endosperm is unsatisfactory, but it does serve to emphasize that it is important to choose grains which are wholly corneous, or almost wholly corneous, if one is to be sure of obtaining good weevil resistance. From Table 6 it will be seen that the 36 D grain has a noticeably poorer corneous shell than the Wiru, SUK 1, or 42 B grains, only 9 per cent. of the grains having a

TABLE 6. *Distribution of Corneous-Endosperm-Shell Thickness in the Varieties used in the Storage Tests. Random samples of 100 grains from bulks tested*

Thickness class (*unit* = $\frac{1}{12}$ *mm.*)	*Wiru*	*SUK 1**	*42 B*	*36 D*	*Okl.44/14*	*B.C.27*
0–0·9	0	1	0	0	9	24
1–1·9	0	1	0	0	6	25
2–2·9	0	1	1	0	13	19
3–3·9	0	0	3	1	18	24
4–4·9	1	6	3	0	17	6
5–5·9	5	3	8	7	25	2
6–6·9	5	5	8	29	9	0
7–7·9	6	10	8	28	2	0
8–8·9	6	9	7	19	1	0
9–9·9	6	5	10	7	0	0
10–10·9	5	8	15	0	0	0
11–11·9	19	15	10	2	0	0
12–12·9	22	16	14	4	0	0
13–13·9	18	11	8	2	0	0
14–14·9	6	8	4	1	0	0
15–15·9	1	1	1	0	0	0

* The SUK 1 was unfortunately adulterated with a little B.C.27 during the threshing: the three grains in the classes 0–2·9 are almost certainly B.C.27, and not SUK 1. As there was no other material available, and the slight adulteration would have biased the tests against SUK 1, it seemed legitimate to use it.

shell thickness greater than 10 eyepiece units: whereas these three varieties which showed good weevil resistance have from 52 to 71 per cent. of their grains with a shell thickness of 10 units or more.

The combination of earliness of maturity with a weevil-resistant grain has been obtained: but there is room for improvement in yield: that of SUK 1 has been disappointingly low in several parts of the Territory.

Other disadvantages have also come to light: SUK 1 is very susceptible to covered smut (*Sphacelotheca sorghi*); 36 D and 42 B have not yet been tested against this disease. The rather wet conditions in the 1955–6 season have shown that these grains of Wiru origin weather badly, the corneous endosperm is degraded, and the grain becomes soft. The progeny of other crosses with corneous grains (B.C.27 (2) × Msumbiji and B.C.27 (2) × Belko backcrosses) show signs of being better in this respect.

Acknowledgements. The author is indebted to the Director of Agriculture for permission to publish this work: to Sir Joseph Hutchinson, to J. E. Peat, and other Empire Cotton Growing Corporation staff at Ukiriguru for help and advice: and to the African Recorder staff who assisted with the storage tests and yield trials.

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(*Received 29 March 1957*)

VARIETAL DIFFERENCES IN THE TENDENCY OF WHEAT TO SPROUT IN THE EAR

P. S. WELLINGTON AND V. M. DURHAM

(*Official Seed Testing Station, Cambridge*)

Summary

The proportion of sprouted grains in different wheat varieties has been determined in field trials and laboratory tests, and is considered in relation to the climatic conditions and the degree of maturation. Differences in maturation occurred among the varieties with white grains, which all sprouted readily under favourable conditions in the field. Maturation was less advanced in certain varieties with red grains, which did not sprout so readily; in other red-grained varieties the degree of maturation was similar to that of varieties with white grains, although the tendency to sprout was less. Varietal differences in the proportion of mature grains which sprouted in the field also suggest that factors such as the rate of germination, and the effect of the glumes, may determine the tendency of a variety to sprout in the ear when conditions of water supply are not optimal.

THE value of wheat is reduced when the covering layers have been ruptured and the embryo exposed in a proportion of the grains, by premature germination, or 'sprouting' in the ear, during wet weather before harvest. In 1941 and 1944 widespread damage was attributed by Greer and Hutchinson [1] to the greater tendency of several popular varieties, especially among the white wheats, to sprout in the ear. Subsequent investigations by Hutchinson, Greer, and Brett [2] confirmed that varieties with white grains sprouted more readily in the ear than those with red grains and showed that they reach a more advanced stage of maturation at the time of harvest. But there were also differences among varieties with the same coloured grains, which appeared to depend on external conditions as well as maturation.

Further observations have now been made on the tendency of certain wheat varieties to sprout in the field and an attempt has been made to determine the critical conditions. Varietal differences in maturation have been determined by laboratory tests under optimal conditions; and, in two varieties, the rate of germination of mature grains, and the effect of the glumes, has been investigated at different levels of water supply.

Sprouting under Field Conditions

It seemed probable that material differences among varieties, in the damage caused by sprouting in the field, would be most apparent when they had been exposed to a wide range of climatic conditions during ripening and harvest. For a preliminary investigation threshed samples of the white wheat Juliana and the red wheat Bersée were obtained from 13 yield trials, at 6 centres, over the period 1946–9 and the percentage of sprouted grains was determined in each case. The results showed that damage from sprouting was negligible in both varieties in the 7 trials in

[Empire Journ. of Exper. Agric., Vol. 26, No. 101, 1958.]

1947 and 1949, with a mean percentage of 0·3 for Juliana and 0·6 for Bersée. By contrast, in only one of the 6 trials in 1946 and 1948 was the percentage in both varieties less than 5; for Juliana the mean percentage was 18·7 and the maximum 40·2, while for Bersée the mean was 7·9 and the maximum 13·6. Thus, when the climatic conditions were favourable for sprouting, the variety with white grains suffered more than twice as much damage as the variety with red grains.

After wet weather during harvest in 1954, ears of 10 winter wheat varieties (4 with white grains and 6 with red grains) were obtained from

TABLE 1. *Sprouting in 10 Wheat Varieties in 1954; the results of 8 Field Trials grouped according to the percentage of Sprouted Grains*

Variety	*Percentage of sprouted grains*						
	less than 5	*5·0–9·9*	*10·0–19·9*	*20·0–29·9*	*30·0–39·9*	*40·0–49·9*	*50·0–59·9*
WHITE							
Staring	5	1	1	..	..	..	1
Holdfast	5	2	..	..	..	1	..
Juliana	6	1	..	..	..	1	..
Victor	4	3	..	..	1	..	..
RED							
Bersée	5	2	1	..	..	..	..
Squarehead's Master	6	1	1	..	..	..	..
Redman	6	1	1	..	..	..	..
Yeoman	7	1	..	..	..	..	..
Hybrid 46	8	..	..	..	..	..	..
Cappelle Desprez	8	..	..	..	..	..	..

8 trial centres; and in each case the percentage of sprouted grains was determined in a random sample of 500 taken from 30 ears. The results for each variety at the different centres have been grouped in Table 1 according to the percentage of sprouted grains. The number of centres at which sprouting exceeded 5 per cent. in a particular variety may be taken as one indication of its tendency to sprout; on this basis the varieties fall into a series with the white wheat Victor, which exceeded 5 per cent. in 4 trials out of 8, at one end, and the red wheats Hybrid 46 and Cappelle Desprez, which did not exceed 5 per cent. at any centre, at the other. But between these two extremes there was no clear-cut difference between the behaviour of the other white and the red varieties. However, when the maximum percentage of sprouted grains in any trial is considered instead, the varieties fall into two distinct groups; those with white grains all had more than 30 per cent. of sprouted grains and none of those with red grains exceeded 20 per cent. These results confirm the particular susceptibility of varieties with white grains, as a group, to sprout in the field when conditions are favourable; and also indicate differences of smaller magnitude between individual varieties, especially those with red grains.

The total rainfall and sunshine in August at each centre are shown in

Table 2, together with the mean percentage of sprouted grains in the white and in the red varieties. It is clear that these factors alone do not account for the marked differences between centres; for example, there was less rain and more sun at Sprowston, where sprouting in the white wheats was 43·4 per cent., than at Askham Bryan, where it was 9·4 per cent., and at Boghall, where it was 4·2 per cent.

Continuous records of rainfall, temperature, and humidity were being kept in a crop of the white variety Holdfast when sprouting occurred, during wet weather, at the start of ripening in 1951. In the lower halves of the ears the grains were still green and only 2 per cent. had sprouted, compared with 11 per cent. in the top halves where they had already

TABLE 2. *Mean Percentage of Sprouted Grains in 4 White Varieties and 6 Red Varieties, in each Trial; with total Rainfall and Sunshine in August*

Trial centre	*Mean sprouting (%)*		*Rainfall (inches)*	*Sunshine (hours)*
	WHITE	RED		
Askham Bryan	9·4	4·4	6·6	85
Boghall	4·2	4·1	5·7	100
Cambridge	2·4	0·9	3·6	151
Newport	1·4	0·9	3·8	125
Seale-Hayne	0·7	0·4	4·2	168
Sparsholt	1·0	1·5	3·8	139
Sprowston	43·4	3·5	5·1	118
Sutton Bonington	4·1	4·2	4·0	115

changed colour. The weather conditions during the week which preceded sprouting on 14 August are indicated in Fig. 1. On 7, 8, and 9 August the weather was fine with daily fluctuations in temperature and relative humidity which resulted in the atmosphere reaching saturation for 8 hours each night. A heavy shower on 10 August saturated the atmosphere during the morning and, after intermittent rain in the afternoon of 11 August, it remained saturated for a continuous period of 16 hours on 12/13 August, at the end of which sprouting had occurred. Similar conditions have been reported by Harrington and Knowles [3] who found that sprouting had occurred after a 5-day period with an average temperature of 61·4° F. and relative humidity of 81·7 per cent., which included 2·16 in. of rain during one 24-hour period.

It appears that the climatic conditions responsible for sprouting are sufficient rain to saturate the ear followed by a period of high atmospheric humidity to allow the transfer of moisture from the glumes to the grain. It has been shown that heavy rain by itself is not enough, if the evaporating power of the atmosphere increases rapidly as soon as it has stopped, because the moisture held in the chaff is then lost to the atmosphere without appreciably raising the moisture content of the grains [4]. This would suggest that the relatively low percentage of sprouting, at some centres with a high total rainfall in August 1954, was due to the short duration of the period of high humidity following rain; this is likely to be the critical factor in the field.

Sprouting in Laboratory Tests

The proportion of grains which have acquired the ability to germinate in the ear at a given stage of ripening is determined by the process of maturation [5] and will be indicated by the percentage which sprout when all external conditions are optimal for germination. In order to investigate varietal differences in maturation a laboratory test was evolved in which sprouting was induced by first soaking the ears and then

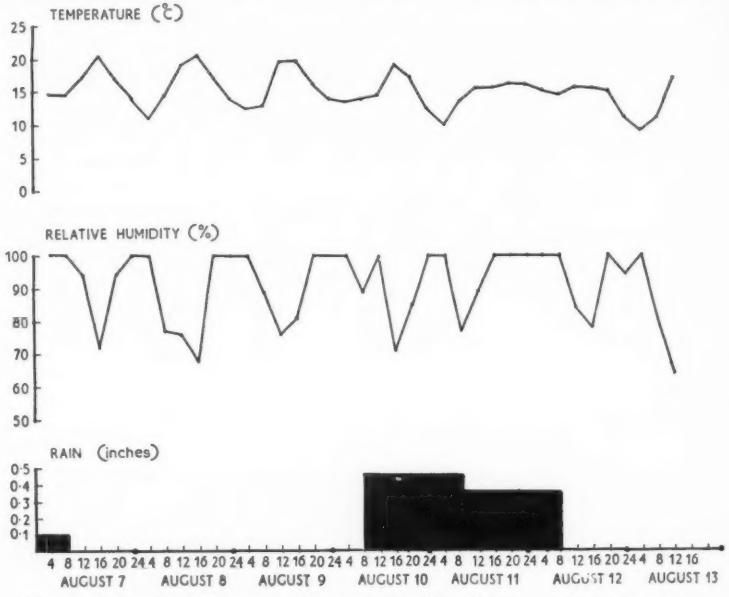

FIG. 1. Records of Temperature, Relative Humidity, and Rain for 7 days before sprouting

incubating them in a saturated atmosphere [4]. After 120 hours the grains were removed from the ears and examined for germination, as this was the time required for almost complete sprouting in the white variety Holdfast when ripe for harvest.

Ears of the same varieties, which had been examined for sprouting in the field, were subjected to laboratory tests at one centre in 1954 to determine whether varietal differences in maturation could be directly related to the proportion of sprouted grains. Owing to wet weather, the moisture content of the grains when harvested was higher than normal (25–40 per cent. of dry weight); an additional series of tests was therefore made after the ears had been kept for 3 days in an unheated greenhouse, which reduced the moisture content to normal (12–14 per cent.). The results shown in Table 3 indicate differences in the maturation of the varieties before and after the final reduction in moisture content. The two white varieties, Holdfast and Staring, had reached a more

advanced stage of maturation than Juliana and Victor, and this difference was still apparent after drying, when each of the four varieties increased in germination by 5–10 per cent. Maturation in the red varieties Yeoman and Redman was comparable to that in the white varieties Juliana and Victor before and after drying; but it was less advanced in all the other red varieties. The final desiccation caused a marked increase in the germination of Hybrid 46 and Squarehead's Master but had no effect on that of Cappelle Desprez, at a similar stage of maturation, or on Bersée or Atle, where maturation was very much delayed.

TABLE 3. *Percentage of Grains Sprouting under Optimal Conditions in the Laboratory at the Harvest-ripe Stage in 1954*

Variety	*Percentage sprouting* (*Moisture content 25–40 per cent.*)	(*Moisture content 12–14 per cent.*)
WHITE		
Staring	84·2	91·2
Holdfast	84·6	95·8
Juliana	51·6	62·1
Victor	57·6	67·9
RED		
Bersée	21·8	18·6
Squarehead's Master	17·2	52·1
Redman	54·8	74·5
Yeoman	50·8	72·0
Hybrid 46	35·2	59·6
Cappelle Desprez	48·6	42·4
Atle	4·2	6·0

When these tests are considered in conjunction with the data in Table 1 it appears that for some varieties the proportion of grains which had reached maturity was greater than that of those which actually sprouted in the ears. The ratio of sprouted to mature grains was high for the white varieties, at the most advanced stage of maturation, and for the red varieties where maturation was least; but in the other red varieties the ratio was lower. These results were confirmed for the same varieties in 1956 when laboratory tests for maturation were made before and after sprouting had occurred. Both the percentage which sprouted under natural conditions, and the percentage which sprouted under optimal conditions, are shown in Table 4 for ears which were harvested on 8 August and 23 August; and the ratio of sprouted to mature grains has been calculated for the second test. Probably because of unusually low temperature, and high humidity during ripening, the maturation in most varieties was less advanced than in 1954; and there was only a relatively small increase between the tests.

There were very marked differences among the white varieties both in the stage of maturation, as shown by the laboratory tests, and in the sprouting under natural conditions. But although sprouting was greatest in Holdfast, which was most mature, and least in Juliana, which was also

less mature, there was also a considerable difference in sprouting between Staring and Victor, which had both reached approximately the same stage of maturity. The ratio of sprouted to mature grains was therefore high for Holdfast and Victor but low for Staring and Juliana. The differences in sprouting among the red varieties were less although there were marked differences in maturation. The ratio of sprouted to mature grains was similar for the varieties Bersée, Squarehead's Master, Redman, and Hybrid 46, but was very much less for Yeoman and Cappelle Desprez than for the white varieties.

Taken together the results in 1954 and 1956 suggest that although

TABLE 4. *Percentage of Grains Sprouting under Natural Conditions in the Field, and Optimal Conditions in the Laboratory, on two dates during ripening*

Variety	8 August		23 August		
	Field	Lab.	Field	Lab.	Ratio sprouted: mature
WHITE					
Staring	0·6	49·6	5·4	65·4	1:12·1
Holdfast	0·4	88·0	43·0	95·2	1: 2·2
Juliana	0	24·2	2·0	39·0	1:19·5
Victor	0·6	50·8	21·4	58·7	1: 2·8
RED					
Bersée	2·4	56·5	6·6	49·6	1: 7·5
Squarehead's Master	1·4	14·0	3·2	15·5	1: 4·9
Redman	0	38·0	8·6	51·9	1: 6·0
Yeoman	0	50·9	1·8	56·0	1:31·0
Hybrid 46	1·2	30·0	3·8	31·5	1: 8·3
Cappelle Desprez	1·4	29·1	1·0	30·4	1:30·4

early maturation predisposed certain white varieties to sprout, and lack of maturation limited sprouting in certain red varieties, other factors determined the level of sprouting in the field by controlling the germination of the grains which had already reached maturity.

Germination of Mature Grains and the Effect of the Glumes

The observations on the climatic conditions in which sprouting occurred in the field (Fig. 1) suggested that the critical factor was the amount of water available for germination. This depends ultimately on the rainfall, as the only external source of supply, but will be determined by the difference between the rate of absorption by the embryo and the rate of evaporation into the atmosphere. Varietal differences in the physical properties of the glumes, and the covering layers of the grains, which affect these rates, may therefore influence the extent of germination, especially when the level of water supply is a limiting factor. They might also account for the difference between germination of grains in the ear, and after removal, which have been reported in some varieties [2], [6]. These factors were investigated in comparative germination tests with fully mature grains of the white variety Holdfast and the red

variety Atle. The two basal grains in spikelets from one side of the ear were left in their glumes, while those from the other side were removed; sets consisting of 4 × 24 grains were then placed in the individual cells of 'spotting' plates, with different amounts of water, and the percentage which had germinated in each treatment was determined after 24 and 48 hours, and is shown in Table 5.

Without their glumes, the white grains all germinated in 24 hours at levels above 0·03 ml./grain, but fewer red grains had germinated at levels below 0·09 ml./grain, although at higher levels germination was also

TABLE 5. *The Percentage Germination of Mature Grains at different levels of Water Supply, without Glumes (−G), and with Glumes (+G)*

Initial level of water ml./grain	WHITE (*Holdfast*)				RED (*Atle*)			
	24 hrs.		*48 hrs.*		*24 hrs.*		*48 hrs.*	
	−G	*+G*	*−G*	*+G*	*−G*	*+G*	*−G*	*+G*
0·01	1	0	1	0	0	0	0	0
0·02	41	25	87	71	20	2	97	67
0·03	86	52	100	94	45	12	100	80
0·05	100	60	100	100	63	15	100	95
0·09	100	77	100	95	97	42	100	94
0·20	100	63	100	79	99	35	100	69
0·40	100	51	100	76	100	15	100	34

complete. The percentage germination at 48 hours was the same in both varieties at all levels of water supply. This indicated that there was a varietal difference in the rate of germination of the naked grains, at levels of water supply below the optimum; and that the time required for germination of the white grains was less than that required for the red.

The presence of the glumes reduced the percentage of grains which germinated in 24 hours at moisture levels below the optimum, by a similar amount in both varieties; but at the optimal level and above the reduction was greater in the red variety. The reduction caused by the glumes at 48 hours was also somewhat greater in the red variety at levels below and above the optimum. The rate at which the grains germinated in their glumes was thus very much less in the red variety than in the white; and this effect was due partly to the inherent difference in the rate of germination, and partly to the presence of the glumes. When the supply of water was limited, the reduced rate of germination was associated with a lower moisture content in the grains, which had to compete with the glumes for the available water; but this was not so at excessive levels of water supply when the retention of coherent films of water between the glumes and the grain probably impeded the diffusion of oxygen to the embryo. Under field conditions these effects would reduce sprouting in the red variety to a greater extent than in the white, when either the amount of the initial rainfall or the duration of the subsequent period of high humidity resulted in an amount of water available for germination which was below the optimum.

The possibility that the glumes contained a specific germination

inhibitor, suggested by Smith [7], was also investigated. Aqueous extracts were prepared by soaking glumes of both varieties in water for 48 hours and their effect on successive stages of germination was determined at three levels of supply. In excess both extracts appeared to increase the percentage of grains in which the embryos had become imbibed and completely filled the space under the covering layers, during the first 12 hours; they also decreased the percentage of grains in which the primary root had emerged through the coleorhiza at 48 hours. But as the extracts had no effect, at any level, on the percentage of embryos which ruptured the covering layers, compared with the percentage at the corresponding level in water, it appears to be the physical properties of the glumes, rather than any water-soluble substances they contain, which determines their effect on germination.

Conclusion

There are marked differences between wheat varieties, both in the proportion of grains which are capable of sprouting under optimal conditions at the normal time of harvest, and in the proportion which in fact do so when conditions are favourable in the field. In the first case, the proportion is determined by the process of maturation in the particular variety; but in the second case, grains which have in fact acquired the ability to germinate may not do so because the water available for germination is seldom at the optimal level. Under these conditions varietal differences in the germination behaviour of mature grains, and the effect of the glumes, may determine the tendency to sprout.

Acknowledgements. The authors are grateful to Mr. C. C. Brett for much helpful information in the early stages and to Mr. F. R. Horne and Professor F. G. Gregory for continued interest and encouragement.

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(*Received 12 April 1957*)

NOTE ON AN IMPROVED TECHNIQUE IN ESTABLISHING *SETARIA SPHACELATA* FROM SEED

R. C. ANSLOW

(*Department of Agriculture, Mauritius*)

WITH PLATE 2

Summary

Difficulty was experienced in establishing *Setaria sphacelata* due to insect damage of the sown seed. Experimental results show improved establishment from seed dusting with Dieldrin, using 10 gm. active ingredient per kilogramme of seed. No advantage resulted from Arasan seed dusting, nor from Endrin post-emergence spray.

THE value of *Setaria sphacelata* as a fodder grass has become appreciated under a variety of climatic conditions in Mauritius. Propagation of both the Kazungula and Bua River varieties is usually by division of plant crowns, which gives a good stand when soil moisture is reasonably available. However, the labour cost is high and has averaged Rs. 79·80 (120 shillings) per acre on an 8·5 acre field.

Establishment of Setaria from seed has been reported by Botha [1] from South Africa, and it was decided to give direct seeding a trial in Mauritius.

Seed of the Kazungula variety, imported from South Africa, was used on two experimental stations differing in soil type. The resulting stands were very patchy, one of them being a complete failure. Examination of the bad areas showed that red-ant runs followed each drill and empty hulls of Setaria seed were thrown up around ant-nests.

Experimental

A field trial was carried out at Reduit on an area which had previously failed to give a satisfactory stand. The trial, in three blocks, tested the effect of two seed dusts: Dieldrin insecticide at 20 gm. of 50 per cent. powder per kilogramme of seed, and Arasan fungicide at 5 gm. of 50 per cent. powder per kilogramme of seed; and of a post-emergence Endrin spray, using 0·5 lb. active ingredient in 50 gallons per acre, applied at the onset of tillering. The seed rate was 8 lb. per acre, in 3 ft. drills.

Counts of seedling numbers were made 1 month after sowing and the fresh weight of herbage from the first cut, 5 months from sowing, was measured.

Results

Table 1 summarizes the results.

Analysis of the results showed significantly higher seedling numbers and herbage weights from seed treatments incorporating Dieldrin. There was no measurable effect from seed treatment with Arasan nor from Endrin post-emergence spray.

[Empire Journ. of Exper. Agric., Vol. 26, No. 101, 1958.]

Discussion

Seed treatment of *Setaria sphacelata* with Dieldrin insecticide gave greatly improved establishment. The photograph in Fig. 1 (Plate 2) shows a control plot in the centre, the nearest drill being in front of the

TABLE I. *Seedling Numbers and First Harvest Weights*

Seed treatment	*Average no. of seedlings in 3 ft. of drill*	*Fresh weight of grass as lb. per acre*
	S.E.	
Nil	8·1 ± 3·14	2,198
Dieldrin	26·5 ± 1·36	7,419
Arasan	6·7 ± 0·71	2,998
Dieldrin + Arasan . .	28·1 ± 2·65	7,795

first white sheet. The plots to the right of this, and directly behind it, after the last white sheet, were sown with Dieldrin-treated seed.

Observations indicate that control of red ant was the chief factor in giving improved establishment, but it is possible that other insects were partly responsible for the poor stands. Winstanley [2] mentions a wide range of insects which are very susceptible to Dieldrin.

Subsequent to this trial, routine Dieldrin seed-treatment of other grass species has greatly increased the proportion of successful stands.

Acknowledgements. Pest Control (C.A.) Ltd. kindly supplied the Dieldrin and Endrin which were used. Mr. J. H. Julien, Horticulturist, took the photograph (Fig. 1).

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(*Received 26 March 1957*)

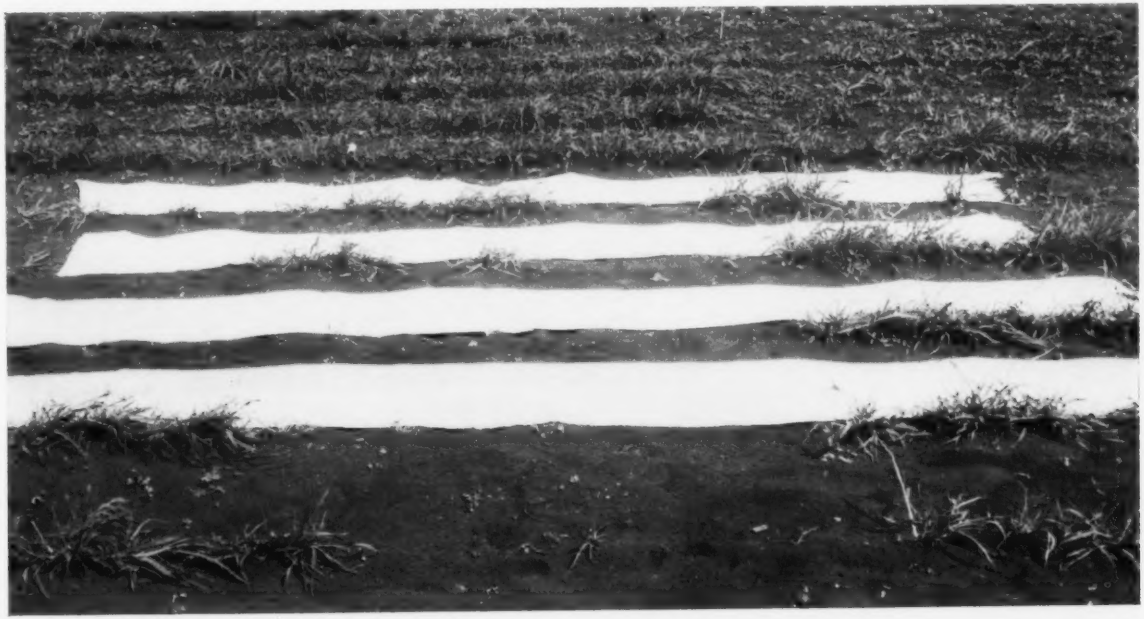

FIG. 1. Effect of seed-treatment on establishment of *Setaria sphacelata*.
Centre foreground: Untreated.
Background and on right: Seed treated with Dieldrin.

SEASONALITY OF BEEF AND VEAL PRODUCTION IN ARGENTINA AND CONSEQUENT BEEF EXPORTS

R. A. MACKNESS

(*School of Agriculture, University of Cambridge*)

Summary

This paper presents data of Argentine beef production and export from 1930 to 1954.

Beef production in Argentina was about half a million tons a year greater in 1949 than it was in 1930. The effect of the droughts in 1950–3 is clearly shown. Seasonality of production became more pronounced in 1950–4, compared with the regular monthly pattern of production in earlier years. Before 1938 Argentine chilled beef arrived in the United Kingdom very regularly each month. Between 1949–54 exports of frozen beef from Argentina were markedly seasonal, but were below the general monthly average in the months when United Kingdom home production was seasonally above the monthly average.

THIS paper, in continuation of this series on beef [1], presents data of seasonality of production and consumption of beef and veal in Argentina and the effect such seasonality has on the supply of beef and veal for the British market.

Argentina is favoured climatically with conditions which, with highly fertile land, have allowed beef and veal production to expand during the last seventy years in response to increasing demand, both internally and in the export market. Production is, however, vulnerable in that in seasons of low rainfall there is a lack of grazing and consequently a lower level of output.

The cattle population in Argentina was relatively stable between 1930 and 1942, varying between 30 and 34 millions. There has been a spectacular increase in cattle numbers since 1942, when the cattle census gave a population of 31·5 millions. By 1952 there were said to be 45·3 million cattle. More recent estimates suggest that the population is still increasing and may be expected to increase further if economic conditions are favourable.

Statistics of Argentine total production, consumption, total exports, and exports to the United Kingdom, between 1930 and 1954, are given in the Appendix. The potential of the Argentine beef industry is illustrated by the annual production achieved in 1947, 1949, and 1950, although the effect of the drought is seen in the production for 1952 and 1953. Of great significance for the United Kingdom meat market was the large increase in Argentine home consumption, which averaged 1,051,000 tons a year between 1930 and 1939, increased to 1,200,400 tons a year between 1940 and 1949, and was 1,549,000 tons a year between 1950 and 1954.

Although production increased it did not do so as fast as consumption and the inevitable result was a decline in the exportable surplus. Exports which averaged 411,000 tons a year between 1930 and 1939, were

[Empire Journ. of Exper. Agric., Vol. 26, No. 101, 1958.]

300,000 tons a year between 1940 and 1949, and had fallen to an average of 121,400 tons a year between 1950 and 1954.

Until 1939 the United Kingdom usually received more than 80 per cent. of the total Argentine beef exported. It is not surprising, therefore, that the decline in the exportable surplus greatly affected exports to the United Kingdom. Between 1930 and 1938 the annual average beef export to the United Kingdom from Argentina was 364,000 tons. This average was slightly inflated by the high level of deliveries in 1930, 1931, and 1932 before the Ottawa Agreements, but Argentine supplies to the United Kingdom seemed to have settled down to about 350,000 tons a year just before 1939.

Data of exports to the United Kingdom are not available for the period 1939–45 inclusive, but total exports declined from 456,750 tons in 1939 to 171,500 tons in 1945. Between 1946 and 1949 exports to the United Kingdom averaged 201,700 tons a year, but they declined to an average of 84,300 tons a year between 1950 and 1954.

Argentine Production

The major part of Argentine beef production is consumed internally and, as the population has increased, increases in production have been absorbed by the home market. The annual average production between 1930 and 1934 was 1,522,000 tons, between 1935 and 1939 it was 1,736,000 tons, an increase of 14 per cent. Between 1940 and 1949 annual production varied from 1,430,550 tons in 1945 to 2,031,000 tons in 1949. From 1950 to 1954 production averaged 1,829,000 tons annually, but these years were affected by drought and political troubles.

It is unfortunate that data in sufficient detail are not available to allow an analysis of seasonal variation of the total production of Argentine beef before 1939.

However, an analysis of sales of cattle at Liniers[1] is possible for periods between 1936 and 1954, which indicates the pattern of Argentine beef production in that sector of the industry which is most closely connected with exports. The data in Table 1 show the indices of seasonal variation of cattle sales for four periods, one pre-war, one during the war, and two post-war.

Cattle sales at Liniers increased from a total of 2,096,700 head in 1936 to 2,328,200 head in 1938. In 1943 sales reached 2,557,100 head, but declined to 2,227,400 in 1944. Increased sales occurred after 1945 and had reached 3,496,200, 3,536,800, and 3,654,900 head in 1948, 1949, and 1950 respectively. This advance was halted by the effect of low rainfall and increasing political uncertainty in 1951, 1952, and 1953, so that by 1953 no more than 2,048,300 head of cattle were sold at Liniers.

Between 1936 and 1938 sales at Liniers were very level from month to month, with peak sales in March and April. The period March to July inclusive was above the general average of 100. The only other month of above-average sales was in December. By 1942–4 peak sales were concentrated in the months January to May inclusive, and the

[1] Liniers is the cattle market in Buenos Aires.

standard deviation was only slightly higher than for the indices for 1936–8. Between 1948 and 1950 above-average levels of sales occurred in March, May, and June and in August to November inclusive. There was thus a tendency for above-average sales to be scattered throughout the year instead of being concentrated in the first half of the year. The pattern of production, however, remained relatively smooth with a standard deviation of only ±9·4.

TABLE 1. *Indices of the Average Monthly Sales of Argentine Cattle at Liniers in 1936–8, 1942–4, 1948–50, and 1951–3*

Period	*1936–8*	*1942–4*	*1948–50*	*1951–3*
Month				
January	98·9	101·4	91·2	113·3
February	92·1	107·9	83·2	85·1
March	109·5	121·6	111·5	90·7
April	108·6	102·8	94·2	135·4
May	102·0	106·3	105·0	123·6
June	101·3	99·3	109·9	118·4
July	104·8	93·6	96·4	115·6
August	95·8	88·7	110·0	67·2
September	97·3	94·9	104·7	60·4
October	89·8	92·6	100·2	97·5
November	94·8	94·3	102·1	97·6
December	105·1	96·6	96·1	95·2
Average	100·0	100·0	100·0	100·0
Standard deviation ±	6·0	8·5	9·4	21·5
Annual average number sold: '000 head	2,248·7	2,427·5	3,569·3	2,525·9

Annual average sales at Liniers declined by over 1,000,000 head in 1951–3 compared with sales in 1948–50. This decline was accompanied by an increase in seasonal variation, but peak sales were once again mainly concentrated in the period April to July inclusive. Too much emphasis should not be placed on the pattern of sales in the period 1951–3, because they were abnormal years, particularly affected by drought.

Beef- and veal-production data from large abattoirs in Argentina are available for the periods 1943–7 and 1950–4 and are shown in Table 2. Although these data do not completely accord with the data of cattle sold at Liniers given in Table 1, they again relate to that sector most closely concerned with beef for export, namely the *frigorificos* or freezing plants.

In the earlier years, 1943–7, peak production occurred in these abattoirs in two well-defined periods: May, June, and July, and December, January, and February. In the latter years 1950–4 there was only one peak period, April to July inclusive, but the pattern of production in 1950–4 was less smooth than in 1943–7. From the point of view of the United Kingdom market the above average months of production were admirable, since the meat exported from Argentina would tend to arrive

in the United Kingdom at a period of the year when United Kingdom supplies were seasonally below the monthly average.

TABLE 2. *Indices of the Average Monthly Production of Beef and Veal in large Argentine Abattoirs. 1943–7 and 1950–4*

Period	*1943–7*	*1950–4*
Month		
January	109·3	103·6
February	101·0	90·5
March	87·1	93·6
April	91·6	115·0
May	104·1	123·3
June	106·5	119·1
July	114·1	110·6
August	89·8	67·5
September	84·6	78·8
October	77·8	99·1
November	99·3	101·1
December	134·8	97·8
Average	100·0	100·0
Standard deviation ±	3·4	15·5
Annual average production: '000 tons	721·7	858·6

The other determinant of the pattern of exports is the pattern of internal Argentine consumption. Accurate monthly data relating to total Argentine consumption are not available, but a reasonably accurate picture is obtained by considering the data of beef and veal handled by factories and *frigorificos* and destined for home consumption. The even flow of beef and veal for the home market each month and the tendency for total home consumption to increase with the increases in production were marked features of the Argentine beef trade between 1949–54.

Argentine Exports

Before 1939 Argentine chilled beef exported to the United Kingdom market was characterized by its extreme regularity of arrival. In the absence of data of exports before 1939, it is useful to note the seasonal variation of imports of Argentine chilled and frozen beef into the United Kingdom. The figures in Table 3 include the pattern of imports for the years 1934–8 for chilled and frozen beef and veal.

The very smooth pattern of Argentine chilled-beef imports into the United Kingdom provided an average of 29,000 tons of beef each month in 1934–8. In those years the United Kingdom received from Argentina fifty times as much chilled beef compared with frozen beef. The marked seasonal variation of frozen beef imports, therefore, had little effect on the pattern of the total supply of Argentine beef on the British market.

During the period 1939–45 Argentine chilled-beef export ceased and this policy continued until 1954. The pattern of Argentine frozen-beef imports into the United Kingdom between 1946 and 1954 is included in Table 3. Although the indices indicate a marked seasonality of arrival,

most of the beef came into the United Kingdom at times of the year when home-killed supplies were seasonally below the general monthly average. In the months of September to December inclusive only 21 per cent. of the annual import of Argentine beef arrived in the United Kingdom, whereas in the months of January to April 41 per cent. arrived.

TABLE 3. *Indices of Average Monthly Imports of Chilled and Frozen Argentine Beef and Veal into the United Kingdom, 1934–8 and 1946–54*

Month	Chilled 1934–8	Frozen	
		1934–8	1946–54
January	110·0	146·4	107·4
February	92·2	131·2	154·1
March	106·0	148·2	115·6
April	100·1	56·8	114·4
May	97·7	48·4	97·8
June	94·7	84·9	128·0
July	95·1	68·4	124·6
August	95·2	64·0	107·6
September	100·3	71·9	95·3
October	102·5	186·4	63·0
November	105·5	82·7	43·1
December	100·7	110·7	49·3
Average	100·0	100·0	100·0
Standard deviation ±	5·1	42·0	32·0
Annual average import; '000 tons	348·0	6·9	148·4

Statistics of total Argentine beef exports are meagre, but those published in the *United Nations Monthly Statistical Bulletin* provide the data for the analysis of seasonal variation for the years 1949–54 shown in Table 4.

TABLE 4. *Indices of the Average Monthly Exports of Argentine Beef, 1949–54*

Month	1949–54
January	125·2
February	78·2
March	141·9
April	130·2
May	101·1
June	121·1
July	120·1
August	66·6
September	79·7
October	58·1
November	70·5
December	107·3
Average	100·0
Standard deviation ±	27·1
Annual average exports; '000 tons	133·3

A marked pattern of seasonal variation of total beef exports to all destinations was a feature of that period. The shipments in the months August to November, when only 23 per cent. of the annual average was exported, were well below the general monthly average. This quantity coincides closely with the 21 per cent. of Argentine beef arrivals in the United Kingdom in the months September to December inclusive, if allowance is made for transit time.

The pattern of Argentine beef exports 1949–54 was more seasonally varied than it was before 1939, mainly because in the later period chilled-beef exports were absent, the exportable surplus was smaller due to the increased Argentine consumption, and Argentine production became more seasonally varied. Thus, in the presence of the continuing smooth pattern of Argentine internal consumption, the exportable surplus became increasingly seasonally varied.

Although it is not the purpose of this paper to consider what has occurred since meat was freed from control in the United Kingdom in July 1954, British producers should note carefully the regularity of chilled-beef imports from Argentina immediately preceding 1939. The quantity of those pre-war imports is also of significance, being more than twice the annual average quantity imported during 1946–54.

It is desirable that steps be taken to ensure that the United Kingdom beef market does not suffer from above-average imports when home production is seasonally above the average. What has happened in the United Kingdom beef market and in overseas supplies since meat was freed from control in the United Kingdom in July 1954 will be the subject of a further paper in this series.

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APPENDIX

Argentine Beef and Veal Production, Consumption, and Exports, 1930–54

Year	*Production*	*Consumption*	*Total exports*	*Exports to U.K.*
		Thousands of tons		
1930	1,559·90	1,061·00	437·20	388·80
1931	1,460·30	977·00	429·00	398·50
1932	1,470·30	1,026·00	400·75	386·30
1933	1,512·10	1,082·60	375·55	358·40
1934	1,607·05	1,171·85	375·10	352·05
1935	1,684·65	1,242·10	372·25	351·50
1936	1,705·85	1,243·65	390·85	360·10
1937	1,752·85	1,104·30	434·60	350·20
1938	1,716·25	1,116·70	438·15	349·00
1939	1,820·70	1,131·85	456·75	*
1940	1,698·35	1,112·25	367·65	*
1941	1,854·35	1,113·90	371·05	*
1942	1,732·80	1,022·00	371·50	*
1943	1,610·35	989·20	292·10	*
1944	1,593·90	1,004·30	290·80	*
1945	1,430·55	1,062·65	171·50	*
1946	1,668·80	1,232·90	223·45	154·65
1947	2,022·85	1,390·00	332·65	247·95
1948	1,968·40	1,504·35	273·00	188·90
1949	2,031·00	1,573·50	312·80	215·40
1950	2,011·70	1,589·00	170·90	133·10
1951	1,849·70	1,597·80	117·50	56·40
1952	1,760·00	1,488·80	101·10	49·70
1953	1,737·60	1,511·00	113·20	95·40
1954	1,786·20	1,558·50	104·20	86·90

* Not available.

(*Received 25 April 1957*)

THE INFLUENCE OF NITROGEN, PHOSPHORUS, AND POTASSIUM NUTRITION OF FLUE-CURED TOBACCO ON THE INCIDENCE OF CERCOSPORA LEAFSPOT DISEASE[1]

R. C. STEPHEN

(*Tobacco Research Board of Rhodesia and Nyasaland*)

Summary

The influence of the nitrogen, phosphorus, and potassium nutrition of flue-cured tobacco on the incidence of Cercospora leafspot disease (*Cercospora nicotianae*, Ell. and Ev.) was examined.

When the barn-spot phase of the disease was checked by the use of high yellowing temperatures and humidities during curing, the disease incidence was inversely related to the rate of fertilizer nitrogen used. When barn-spot development proceeded unchecked the relationship was direct. The same trends existed with fractional applications of nitrogen, but to a much lesser extent.

The rate of phosphorus or of potassium applied had no effect on the amount of disease, whether barn spots were suppressed or allowed to develop.

MOST of the flue-cured tobacco crop in Southern Rhodesia is produced on soils of a light sandy texture commonly called sandveld. These soils are naturally low in fertility and the application of a 'complete' fertilizer mixture is necessary to secure good yields of high-quality leaf. Experiments were carried out to determine the influence of applied nitrogen, phosphorus and potassium on the incidence of Cercospora leafspot disease (*Cercospora nicotianae*, Ell. and Ev.).

Review of Literature

The influence of the nitrogen, phosphorus and potassium nutrition of tobacco on the amount of frog-eye and barn spot (*C. nicotianae*) does not appear to have received much critical attention. Occurrence of the disease in seed-beds appeared to be dependent on the condition of the plants, according to Hopkins [1], who observed that the disease occurred on seedlings which were turning yellow as a result of nitrogen deficiency. Hopkins [2] further reported that, under Rhodesian conditions, leaf deficient in nitrogen in the field was very susceptible to frog-eye; where tobacco received insufficient fertilizer for normal growth, severe frog-eye infection and large losses of leaf from barn spot resulted.

Hill [3], however, reported that there was no correlation between the quantity or kind of fertilizer and the occurrence of Cercospora leafspot disease on tobacco under Queensland conditions; normal plants, with suitable fertilizer applications, appeared to be less spotted than others nearby; but this was only a temporary condition, as the leaves were just as seriously spotted after curing.

[1] Research paper No. 30, Tobacco Research Board of Rhodesia and Nyasaland, Salisbury, Southern Rhodesia.

[Empire Journ. of Exper. Agric., Vol. 26, No. 101, 1958.]

Norval [4] suggested that the causal organism was unable to establish itself in healthy, dark-green tissue (resulting from an ample supply of nitrogen), but readily attacked leaves which were beginning to turn yellow. Apparently frog-eye could be largely avoided by maintaining good, steady growth.

Material and Methods

Plot size. Plots were approximately 1/50th acre in size and consisted of four rows 3 ft. 6 in. apart, each containing thirty-one tobacco plants spaced at 2 ft. within the row. End plants and outside guard rows were discarded to eliminate border effects.

Fertilizer application. The pre-planting fertilizer was placed on the level ground before ridging, in one continuous band in the 1952–3 season, and in two bands, 8 in. apart, in subsequent seasons. Finally the fertilizer was ridged over with a tractor-mounted disk-ridger. Where post-planting applications were used, the fertilizer was applied in shallow grooves, opened on either side of the ridge.

Disease assessment. Infection by *C. nicotianae* may take two forms. In the first, spots may appear on the leaves in the field; these are generally known as frog-eye spots. In the second, however, brown or black spots (known as barn spots) can develop during curing, from incipient field infection. Accordingly, the assessment of treatment effects was made on the cured leaf, which was sorted into four classes—clean, and light-, medium-, and heavily-spotted, the data being converted into an infection index by using the McKinney Grouping Method [5, 6].

Experimental details. Following preliminary trials carried out in the 1951–2 season, more comprehensive tests were undertaken in the 1952–3 and 1953–4 seasons, with the results reported herein, which fully confirmed those obtained from the preliminary trials.

In the 1952–3 trials temperatures of 85–90° F. at approximately 85 per cent. relative humidity were used to yellow the leaf during curing, conditions which do not restrict the development of barn spot. In the 1953–4 season, however, the leaf was yellowed at temperatures of 100–102° F. with 100 per cent. relative humidity attained by using steam; under these conditions barn-spot development is restricted and very few barn spots appear [7].

The effects of the three main constituents of the fertilizer mixture were examined in factorial arrangements; both rates and times of nitrogen application, and rates of phosphorus and potassium, were studied. Since all interactions were insignificant, only the main effect results are presented. It should be borne in mind, however, that the effects of one constituent were tested over a wide range of the other two.

Sodium nitrate and ammonium sulphate, each supplying 50 per cent. of the required amount of nitrogen, were used as sources of nitrogen throughout. Rates of nitrogen varying from 0 to 46 lb./acre were included. In these and other tests the effect of applying all the nitrogen prior to transplanting was compared with fractional applications given at various times during the growing period. The rates of phosphorus, applied prior to planting as superphosphate, and potassium, applied as

sulphate, were from 40 to 190 lb. P_2O_5/acre and 30 to 170 lb. K_2O/acre respectively.

Results

The results of these trials are shown in Tables 1, 2, 3, 4.

TABLE 1. *Effect of Rate of Applied Nitrogen on the Final Incidence of Cercospora Leafspot on the Cured Leaf*

Rate of N *lb./acre*	*Infection index %*					
	*1952–3**				*1953–4**	
	1	*2*	*3*	*4*	*5*	*6*
0	..	..	..	..	(40·5)†	(34·1)†
15	..	57·8	79·5	77·0	..	..
16	..	..	..	..	29·8	30·9
26	..	..	..	..	26·5	26·6
30	70·1	67·5	83·0	83·3	..	..
36	..	..	..	..	25·1	27·0
45	76·1	76·5	87·0	86·5	..	..
46	..	..	..	..	23·3	24·2
Least significant differences:						
P = 0·05	4·8	8·8	3·2	3·4	4·4	4·6
P = 0·01	..	12·2	4·0	4·5	..	..
P = 0·001	..	..	5·3	5·9	..	..
Mean	73·0	67·3	83·2	82·2	26·2	27·2

* Trials 1 to 4: barn spot not restricted; Trials 5 and 6: barn spot restricted.
† Not included in analysis.

TABLE 2. *Effect of Time of Nitrogen Application on the Final Incidence of Cercospora Leafspot on the Cured Leaf*

Time of application	*Infection index %*				
	*1952–3**				*1953–54**
	1	*2*	*3*	*4*	*7*
All preplanting	71·9	..	83·2	81·7	21·9
Half preplanting, half 21 days after	72·5	67·9	83·0	82·0	18·8
One-third preplanting, one-third at 21 and at 42 days . . .	74·6	66·7	83·2	83·0	19·4
Mean	73·0	67·3	83·2	82·2	20·0

* Trials 1 to 4: barn spot not restricted; Trial 7: barn spot restricted.
All the differences in this Table are not significant at P = 0·05.

The results for the effects of rate of nitrogen, in the different seasons, appeared to conflict with each other; in the 1952–3 trials the final amount of disease on the cured leaf increased progressively with increase in the rate of nitrogen applied, whereas the reverse was true in the following season. The yellowing procedure adopted in the earlier season, however, allowed the development of barn spot, whereas this was restricted in the

TABLE 3. *Effect of Rate of Phosphorus Application on the Final Incidence of Cercospora Leafspot on the Cured Leaf*

Rate of P *lb.* P_2O_5*/acre*	*Infection index %*					
	*1952–3**		*1953–4**			
	3	*4*	*5*	*6*	*8*	*9*
40	83·4	79·5	26·1	27·0	..	..
50	..	..	..	..	19·8	19·5
80	83·3	81·8	25·9	25·4	..	..
100	..	..	..	..	19·1	..
120	82·8	85·4	26·1	28·3	..	21·1
150	..	..	..	..	20·8	..
160	..	..	26·5	28·0	..	..
190	..	..	..	..	..	21·8
Least significant differences:						
P = 0·05	n.s.	3·4	n.s.	n.s.	n.s.	n.s.
P = 0·01	..	4·5	..	..	..	..
Mean	83·2	82·2	26·2	27·2	19·9	20·8

* Trials 3 and 4: barn spot not restricted; Trials 5 to 9: barn spot restricted.

TABLE 4. *Effect of Rate of Potassium on the Final Incidence of Cercospora Leafspot on the Cured Leaf*

Rate of K *lb.* K_2O*/acre*	*Infection index %*						
	*1952–3**			*1953–4**			
	10	*3*	*4*	*8*	*5*	*6*	*9*
30	68·4	81·5	82·4	..	26·6	25·4	20·2
40	..	..	..	18·7	..	..	..
60	71·0	82·9	82·3	..	25·1	28·9	..
90	..	85·1	82·1	..	26·4	26·1	..
100	..	..	..	21·6	..	..	20·7
120	..	..	..	..	26·6	28·3	..
160	..	..	..	19·4	..	..	..
170	..	..	..	..	..	..	21·5
Mean	69·7	83·2	82·2	19·9	26·2	27·2	20·8

* Trials 10, 3 and 4: barn spot not restricted; Trials 8, 5, 6 and 9: barn spot restricted.

All the differences in this Table are not significant at P = 0·05.

1953–4 season by the use of high temperatures and humidities during the yellowing period. It seemed, therefore, that an increase in the rate of applied nitrogen caused a decrease in the number of visible lesions in the field, even though the actual amount of infection may have been high. When barn-spot development was allowed to proceed unchecked the incidence of the disease was increased with increase in the level of applied nitrogen.

Variations in the time of nitrogen application, or in the rates of phosphorus and potassium, had no apparent effect on the disease incidence,

irrespective of the procedure adopted during the colouring phase of curing.

Discussion

The experiments demonstrated that fertilizer nitrogen had a clearly marked effect on the incidence of Cercospora leafspot disease, of a nature dependent on whether or not barn spot was restricted during curing. This agrees with Hill's [3] observations that normal plants grown with suitable fertilizer dressings were less spotted than others nearby, but this was only a temporary condition, since the leaves were just as seriously spotted when harvested and cured. In the 1952–3 trials, where barn-spot development proceeded unchecked, an increase in the disease incidence on the cured leaf was associated with an increase in the rate of applied nitrogen.

In the 1953–4 season barn-spot development was restricted, and therefore the trials carried out under these conditions determined only the treatment effects on the field incidence, despite the fact that the assessment was made on the cured leaf. Under these conditions the disease incidence was decreased with increase in the rate of applied nitrogen. This was in line with Hopkins's [2] and Norval's [4] suggestions that Cercospora leafspot was more prominent on leaf that was deficient in nitrogen and it is probable that these workers based their conclusions on field observations only.

It had been suggested previously by Mandelson [8] and Hill [3] that barn spot resulted only from infection which took place prior to reaping. Accordingly it appeared that an increase in the amount of applied nitrogen in some way depressed the intensity of spotting in the field. The latent infection centres became visible during the curing process as barn spots, provided that their development was not restricted.

It seemed, therefore, that the leaves of plants supplied with ample nitrogen were more susceptible than those of plants to which an inadequate amount of nitrogen was made available. However, in the former, the intensity of field spotting was reduced, and only during curing did the full extent of infection become visible as barn spots.

No reason can be offered to account for the suppression of visible lesion production in the field on infected leaves supplied with ample nitrogen and the development of latent infection as barn spots during curing, a phase of the investigation which warrants further study.

Fractional application of nitrogen, as compared with supplying it in one application before transplanting, did not significantly affect the final incidence of the disease; there was a tendency towards increased spotting with fractional application when barn-spot development proceeded unchecked, though the reverse was true when barn spot was controlled. It appeared that the effects of time of nitrogen application on disease incidence followed the same pattern as that for rate of nitrogen, but to a much lesser extent.

It is possible that the time of nitrogen application would have a greater effect on disease incidence during periods of high rainfall. Such conditions, where there may be a tendency for supplies of available

nitrogen to be leached out, are more prevalent in Rhodesia in the latter part of the growing season; fractional applications of nitrogen would tend to maintain the available nitrogen at a level adequate to prevent nitrogen deficiency. Thus, if barn-spot development proceeded unchecked, an increase in disease incidence might well be associated with an increase in the number of nitrogen applications.

The level of phosphorus or potassium in the fertilizer mixtures apparently had no effect on the final incidence of Cercospora disease on the cured leaf; results were similar whether or not barn-spot development was checked. Brown's [9] suggestion of disease-resistance associated with increased rates of potassium applied to tobacco does not appear to be justified so far as Cercospora leafspot disease is concerned, though such an effect has been found in the case of other tobacco diseases [10, 11].

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(*Received 6 May 1957*)

RESISTANCE TO *CERCOSPORA NICOTIANAE* IN THE GENUS NICOTIANA[1]

R. C. STEPHEN

(*Tobacco Research Board of Rhodesia and Nyasaland*)

Summary

One hundred and thirty-one *Nicotiana tabacum* types of various kinds and twelve other Nicotiana species were found to be susceptible to attack by *Cercospora nicotianae*. No immune material was revealed.

Small differences in degree of infection were found among varieties. The differences were found to be associated with the varietal response to two environmental factors, namely leaf maturity at reaping and the date of transplanting to the land.

THE use of varieties which are immune or highly resistant to one or more disease-producing organisms is a standard method of approach to the problem of disease control in plants. Accordingly a search was undertaken for material resistant to attack by *Cercospora nicotianae* (Ell. and Ev.), the causal agent of frog-eye and barn-spot disease of tobacco in S. Rhodesia.

Review of Literature

Various Nicotiana species have been tested for susceptibility to attack by *C. nicotianae*; according to Hill [1] Heald and Wolf recorded *Nicotiana repanda* (Wild.), as susceptible. Hill [1] showed that twelve species of Nicotiana were readily infected with conidia and mycelium from culture, under greenhouse conditions: Johnson and Valleau [2] used *N. rustica* as a test plant in *C. nicotianae* infection experiments. Although susceptible, *N. triplex* showed some resistance to infection according to Mohr cited by McLean [3]; there were no fewer spots than in less resistant varieties, but the spots were smaller.

There are no records of a completely immune commercial variety of *N. tabacum*.

Hill [1] cited Meurs who claimed to have found evidence of resistance to *C. nicotianae* in certain cigar types of *N. tabacum* in Sumatra, though no varietal resistance was observed in the flue-cured type. The absence of varietal resistance under Queensland conditions was noted by Mandelson [4] and confirmed by Altherton (personal communication). Hill [1] tested three Burley, twelve flue-cured, and eight cigar varieties and demonstrated that the Burley seedlings were very susceptible, the flue-cured types less susceptible, and the cigar varieties were comparatively resistant; varietal resistance of practical importance was not observed in the field.

[1] Research paper No. 33, Tobacco Research Board of Rhodesia and Nyasaland, Salisbury, Southern Rhodesia.

[Empire Journ. of Exper. Agric., Vol. 26, No. 101, 1958.]

McLean [3], employing field observations, noted that the tenth leaf from the top of the plant was almost spot-free in several varieties, in contrast to other varieties; these variations were suggested to be the result of different rates of tobacco-leaf maturation in different varieties. She concluded that evidence for apparent varietal resistance could not be valid independent of leaf-maturity assessment.

In the Belgian Congo, Vekemans (personal communication) recorded several varieties as being less susceptible to leaf spot as a whole and to Cercospora leafspot in particular; the list includes five cigar varieties and two flue-cured varieties one of which, the variety 400, was also named by Clayton [5] as showing resistance to *C. nicotianae*.

In Rhodesia, in a comparison of six varieties, Gold Dollar and White Stem Orinoco were recorded as the varieties with the greatest amount of spotted leaf [6].

Hopkins (personal communication) stated that, under Rhodesian conditions, there was no evidence of varietal resistance. He suggested that any differences in degree of spotting between varieties were determined more by the age of the leaf, degree of ripeness or variation in climatic conditions.

While no sources of complete immunity to attack by *C. nicotianae* appeared to exist, there were indications of some partial resistance. The following study was divided into: (1) susceptibility investigations to determine if any completely immune material existed; and (2) partial-resistance investigations to determine the degree of resistance present.

Susceptibility Investigations

Material was obtained from many sources, and commercial varieties of *N. tabacum*, including flue-cured, Burley, and cigar types, together with miscellaneous oriental, semi-oriental, and native-grown tobaccos, came under observation. In addition, several other Nicotiana species were included.

Seed of all these was sown in seed-beds on marginal land and the plants were allowed to grow to maturity therein. Portions of leaf, apparently infected by *C. nicotianae*, were taken from each variety and species, and incubated on moistened filter paper in Petri-dishes at 26° C. The lesions were finally examined microscopically and the presence of the sclerotial-like knots with conidiophores bearing *C. nicotianae* conidia was accepted as proof of pathogenicity.

Results. A total of 131 types of *N. tabacum* were tested and all were found to be susceptible. The following other Nicotiana species were also susceptible: *N. rustica*, *N. rustica* (Chikwarimba), *N. glutinosa*, *N. sylvestris*, *N. glauca*, *N. gigantea*, *N. petiolaris*, *N. petiolata*, *N. rotundifolia*, *N. solanifolia*, *N. suaveolens*, and *N. multivalvis*. Although not all possible varieties were examined, it was considered that the selection was fairly representative and it seems unlikely that complete immunity will be revealed in any *N. tabacum* varieties. However, many Nicotiana species remain to be tested and there is a possibility of immunity being found among these.

In the absence of material possessing immunity, the search was extended to determine whether any variety possessed a sufficiently high degree of resistance to attack to merit inclusion in a breeding programme.

Partial-resistance Investigations

In the first instance trials were carried out to determine whether the degree of Cercospora leafspot infection varied among different flue-cured varieties. The varieties included in the trials were selected with the primary object of testing their performance with respect to yield and quality; investigation of disease incidence among varieties was initially of secondary importance.

Experimental methods. Plots consisted of two rows of thirty-one tobacco plants, spaced 3 ft. 6 in. between rows and 2 ft. within rows, the plot area being approximately 1/100th acre. End plants were discarded to eliminate border effects.

The incidence of Cercospora leafspot disease was assessed on the cured leaf, which was graded into four categories, namely clean, and lightly-, moderately-, and heavily-spotted leaf, the data being transformed into a percentage infection index using the McKinney Grouping System [7, 8].

Experimental work. Five trials were carried out over three seasons, in which the majority of varieties tested were those allowed by legislation [9] to be grown for commercial purposes. The results of these trials are shown in Table 1.

TABLE 1. *Incidence of Cercospora Leafspot per Variety in Five Trials*

Serial no.	*Variety*	*Infection indices %*					
		1951–2		*1952–3*	*1953–4*		
136	Virginia Gold	..	..	46	10	..	
148	Hicks	..	..	46	14	..	
63	Delcrest	..	42	50	21	19	
25	Yellow Mammoth	55	48	46	..	..	
41	Duquesne	..	47	..	..	..	
93	Daines Bright Leaf	..	..	49	20	..	
180	R. 21	..	..	..	14	19	
71	Meadows Giant	..	..	..	15	..	
M46	Vamorr 50	..	..	..	16	..	
112	C. 7	..	49	55	..	..	
15	Willow Leaf	49	50	..	..	..	
75	White Mammoth	..	51	..	..	..	
12	Jamaica Wrapper	58	48	53	16	23	
1	Bonanza	55	50	54	20	..	
17	White Stem Orinoco	59	56	54	..	..	
183	White Stem Orinoco	..	..	..	18	..	
31	Gold Dollar	62	52	56	..	..	
	Least significant differences						
	$P = 0.05$	5·6	4·8	6·8	n.s.	2·6	
	$P = 0.01$	7·6	6·4	..	..	3·7	
	$P = 0.001$	10·1	8·4	..	..	..	
	Mean	56	49	51	16	20	

Conclusions. Differences in degree of infection appear to exist between varieties, but these were small and do not merit consideration as an indication of resistance. Virginia Gold, Hicks, Delcrest, and Yellow Mammoth appeared to be rather less infected varieties, while Gold Dollar and White Stem Orinoco were consistently the most infected.

Influence of Leaf Maturity on the Disease Incidence–Variety relationship

A study of the data was carried out to determine the cause of the different degrees of infection existing between varieties.

McLean [3], using field observations, suggested that evidence for varietal resistance would not be valid if judged independently of leaf-maturity measurement. It was hoped that this source of error would have been eliminated, or at least considerably reduced, by examination of the disease incidence on cured leaf which was approximately uniformly coloured and ripe when reaped and, theoretically, at the same stage of maturity. However, although leaf of uniform colour is reaped, it does not necessarily follow that such leaf from different varieties is of the same physiological age. Accordingly, an examination of the cured leaf was carried out to determine whether any maturity differences in the field were carried through to the cured leaf or if they had been nullified by the reaping of uniformly coloured leaf.

Method. The larger of the 1951–2 trials was used for this study.

It is general practice to raise the temperature of the barn when most of the leaf has reached the desired degree of yellowing. Consequently, while ripe leaf will have attained the correct degree of colour, over-ripe leaf will be over-coloured and under-ripe leaf will not have coloured sufficiently and will retain some of the original green colour. In the grading system in current use by the Tobacco Research Board of Rhodesia and Nyasaland four grades, namely C3G, L2G, L3G, and TG, are provided for the purpose of placing leaf which retains a certain proportion of green. Since each reaping of all varieties was cured in the same barn, an examination of the percentage green leaf per variety is a valid comparison of the degree of maturity at reaping; the results of this examination are shown in Table 2.

The data in Table 2 indicated that there were significant differences among varieties in the proportion of green leaf and therefore there must have been differences in the degree of maturity at reaping.

A highly significant negative linear relationship was then demonstrated between the percentage green leaf and the observed infection index, which would indicate that leaf which had been reaped before proper maturity would tend to have lower infection indices as a result. The disease-incidence data were therefore adjusted, by analysis of covariance, to determine if the maturity differences at reaping accounted for the variation in amount of infection between varieties (Table 2).

Conclusions. Following adjustment, significant differences among varieties were still present; it seemed, therefore, that differences in leaf maturity at reaping accounted for some, but not all, of the differences in infection indices.

TABLE 2. *Adjustment of Observed Infection Indices per Variety for Differences in Percentage Green Leaf*

Serial no.	*Variety*	*Green leaf %*	*Infection index*	
			Observed	*Adjusted*
63	Delcrest	17	42	45
41	Duquesne	10	47	46
112	C. 7	8	49	48
25	Yellow Mammoth	11	48	48
12	Jamaica Wrapper	13	48	49
1	Bonanza	10	50	49
75	White Mammoth	8	51	50
15	Willow Leaf	11	50	51
31	Gold Dollar	10	52	51
17	White Stem Orinoco	9	56	55
	Least significant differences:			
	$P = 0.05$	4·6	4·8	4·3
	$P = 0.01$	..	6·4	5·7
	$P = 0.001$	..	8·4	..
	Mean	11	49	49

TABLE 3. *Incidence of Cercospora Leafspot on Varieties Transplanted at Different Times*

Serial no.	*Variety*	*Trial 1 1952–3*			*Trial 2 1952–3*	*Trial 3 1953–4*
		9 Nov. (Early)	*1 Dec. (Medium)*	*22 Dec. (Late)*	*25 Nov. (Medium)*	*12 Nov. (Early)*
136	Virginia Gold	33	63	43	58	..
63	Delcrest	34	64	47	60	26
148	Hicks	37	70	31	63	22
12	Jamaica Wrapper	28	77	56	..	..
112	C. 7	42	78	42	..	..
25	Yellow Mammoth	24	78	41	..	..
1	Bonanza	38	78	47	..	..
93	Daines Bright Leaf	33	80	34	..	..
17	White Stem Orinoco	26	81	52	72	15
31	Gold Dollar	29	86	52	72	22
	Least significant differences:					
	$P = 0.05$		11·9		15·3	n.s.
	$P = 0.01$		16·2		20·4	..
	Mean		51		67	21

Influence of Transplanting Date on the Disease Incidence–Variety Relationship

Date of planting is known to influence variety performance in respect of yield and quality [10] and in view of this it was considered possible that the disease incidence–variety relationship might also be affected.

The ten varieties compared in the 1952–3 season were planted at three different times, namely 'early' (9 Nov.), 'medium' (1 Dec.), and 'late' (22 Dec.) and the incidence of Cercospora leafspot disease in rela-

tion to date of planting is given in Table 3. In addition, two variety trials carried out in the 1952–3 and 1953–4 seasons were similarly examined; these trials included many non-prescribed varieties, together with some of the more commonly grown commercial varieties, as checks, but only data from the latter are given in Table 3.

Conclusions. The data demonstrated that varieties react somewhat differently at different dates of planting. According to the comparisons previously discussed (Table 1), Gold Dollar and White Stem Orinoco were consistently the most severely infected. These two varieties, however, appeared to have below-average infection in the early plantings, whereas in the medium plantings their infection indices were in line with previous results.

In the case of Virginia Gold, Delcrest, and Hicks, however, the converse is true; in early plantings these varieties had above-average infection, whereas their infection indices for the medium plantings were below average.

It would appear, therefore, that the degree of Cercospora leafspot infection in some varieties is influenced to some extent by the date of transplanting.

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(*Received 6 May 1957*)